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THE STARRED BIOLOGISTS[1]

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OF the 2,607 scientists starred in one or more of the 7 editions of "American Men of Science" (1906–1944), 257 were starred in botany and 377 in zoology. Thus biologists comprise almost one fourth. Of these, 260 were starred in 1903 and about 62 (25 botanists and 37 zoologists) at each of the other starrings except that in 1920 when, in adjustment to the delay caused by World War I, 72 were starred. Six of the botanists are women and 17 of the zoologists. Foreign-born were 23 botanists and 44 zoologists. Of the botanists, Canada yielded 7, Britain 4, Germany 3, Scandinavia 3 and Asia 5. Of the zoologists, Germany yielded 11, Canada 8, Russia 7, Britain 5, Switzerland 3 and Asia 4. One starred zoologist (E. E. Just, 1883–1941) was a Negro.

The median age when they were first starred has recently been for the botanists about 49 and for the zoologists about 44. For the starrings of 1903 and 1909 the median age of both botanists and zoologists was almost the same, about 40. Hence the average age of winning a star has increased notably, most for the botanists.

Starred relatively young were two botanists starred at 29, 3 zoologists starred at 28 and 4 at 29. (By contrast, 15 mathematicians and 19 physicists were starred before they were 30.) Since the first starring, when several

[1] This article is based on "Scientists Starred 1903–1943 in 'American Men of Science,'" Johns Hopkins University Press, in press.

elderly biologists were starred, only 6 botanists have been first starred when older than 60; the oldest were 63, 65, 67 and 69. Of the zoologists first starred since 1903, 4 were older than 64; they were 66, 68, 77, 78.

Collegiate Training

In the collegiate training of botanists, the leaders have been, for totals, Harvard 22, Cornell 17, Michigan 15, Nebraska 14, Michigan State and Wisconsin 8, Illinois 7, Stanford and Wabash 6, Chicago, Oberlin, Pennsylvania and Syracuse each 5, and California, Iowa State, Kansas State, Minnesota, Missouri and Yale 4. Five institutions graduated 3 each (Columbia, Hanover, North Carolina, Vermont, Toronto); 17 two each and 47 one each. Among the 4 most productive schools, Cornell, Harvard, Michigan and Nebraska, approximately half of the totals were starred in 1903. However, these 4 schools stood high likewise as to the younger botanists, as did also Chicago and Wisconsin.

As to the type of American college from which the starred botanists graduated (bachelor's degree): 45 came from small colleges, 86 from state universities, 25 from state colleges (including 3 from state normals), 79 from endowed universities. About 93 graduated from an institution which included a school of agriculture. However, the University of Michigan and Harvard, without such schools, were two of the three leaders.

As to trends in college training: The small colleges graduated a larger share of the botanists born before 1850 and in the 1880's than of those born in other decades. The state universities graduated about a third of the older groups, but about half of those born in the 1860's and 1890's. Endowed universities have graduated nearly one third of each decade-group. Harvard stood highest as to the older groups, graduating only three of the 40 born since 1889. Michigan graduated 2 or 3 of each of the decade-groups except the 1900's, 3 since 1889. Nebraska graduated none of those born before 1860 and only

one after 1889; 5 (one twelfth) of those born in 1860's and 4 or 3 in the following two decades. Foreign institutions gave collegiate training to 10 botanists, 4 of whom were born in the 1870's and 2 each in the 1850's, 1860's and 1890's.

Thirteen of the starred botanists had no regular degree. Of these, a third were born before 1850, all but 2 before 1870; none since 1879.

Considerably more than two thirds of the starred botanists had their college work in institutions which had at the time a botanist professor starred either then or subsequently.

In the training of starred botanists, teachers who merit especial mention for their success include: L. H. Bailey, C. E. Bessey, W. J. Beal, J. M. Coulter, W. G. Farlow, R. A. Harper, D. S. Johnson and V. M. Spalding. Almost without exception, however, even these exceptionally stimulating men declined badly in their output of subsequently starred students as they aged, the decline commencing usually when they were still in the fifties.

J. M. Coulter's record is especially noteworthy. As a teacher, successively at Hanover, Wabash, Lake Forest and Chicago, he played a large role in the undergraduate training of about a dozen subsequently starred men. (At Chicago, he gave graduate training to more than two dozen additional.) Moreover, his text-books and other writings stimulated many who were not privileged to attend his classes.

Zoology

The zoologists have received their college degrees at about 110 American colleges and universities, 60 of which yielded one, 16 two each, 7 three each, 6 four each and 3 five each. Institutions with most such graduates are Harvard 31, Cornell 16, Indiana 12, Michigan 11, Stanford 10, Williams 10, Columbia and Yale 9, Chicago 8, Amherst, Dartmouth, Hopkins, Kansas and Pennsylvania each 7 and C.C.N.Y., M.I.T., Minnesota, Princeton, Syracuse and Wesleyan each 5 or 6; those with 3 or 4 are:

Bates, Bowdoin, Brown, California, Colby, DePauw, Iowa, Missouri, Oberlin, Ohio, Ohio Wesleyan, Rutgers, Texas. For the zoologists starred 1932–43, the leaders are Cornell 8, Stanford 5, Amherst 4, Chicago, Columbia, Indiana and Missouri 3 each. Sharp declines as to the younger as compared with the older zoologists occurred at Harvard, Michigan, Princeton, Williams and Yale. These institutions graduated 5 to 18 of the older group but only 0 to 2 of the younger. Relatively sharp declines among less productive institutions occurred at California, Hopkins, M.I.T., Wesleyan. Of interest is the fact that most of those who had their collegiate work abroad are relatively young, nearly all immigrants. A total of 32 zoologists had no college degree.

The small colleges and endowed universities held a comparatively high position in collegiate training of zoologists. The state universities were surpassed in each decade, most conspicuously as to the older and youngest zoologists.

The number of collegiate graduates at Harvard who subsequently were starred in zoology is large for the first starring partly because of the highly stimulating influence of Louis Agassiz. He is credited with influencing many to become zoologists, and of attracting to Harvard several already interested in zoology. Cattell lists ("American Men of Science" 3, p. 788) the following as trained under Agassiz: Brooks, Hyatt, Jordan, Lyman, Minot, Morse, Packard, Putnam, Scudder, Shaler, Verrill, Whitman, Wilder.

W. K. Brooks, D. S. Jordan and C. O. Whitman later were especially stimulating teachers, each with several starred men to their credit.

The 144 zoologists who filled out the 1946 questionnaire listed many persons as especially stimulating to them. Those listed by 5–9 are W. K. Brooks, T. H. Morgan, G. H. Parker, W. M. Wheeler and E. B. Wilson. Listed by 3 or 4 are J. H. Comstock, C. A. Kofoid, J. G. Needham, A. S. Pearse and H. B. Ward.

Doctoral Training

Botanists: Ten American universities have conferred doctorates (not honorary) upon 5 or more subsequently starred botanists, namely California 5, Chicago 28, Columbia 15, Cornell 20, Harvard 34, Hopkins 12, Michigan 8, Minnesota 5, Washington (St. Louis) 7, Wisconsin 9. Universities conferring doctorates on 4 are Missouri, Nebraska, Pennsylvania and Yale. German universities conferred doctorates on 16, other European universities on 5.

In the doctoral training of botanists Harvard led by a wide margin for the group starred in 1903 and tied for leadership for the groups of 1909, 1921, 1932 and 1943. Chicago led as to the 1909 and 1937 starrings, tied for leadership in 1932, and stood second in 1927. Columbia led for the 1927 group, stood second for that of 1903. Cornell tied for leadership for the 1943 group and for second place for that of 1909, and for third for those of 1903, 1932 and 1937. Others which stood fairly high recently are Hopkins, Missouri, Pennsylvania, Wisconsin. Of those starred in 1903, 13 had European doctorates; of the 1921–1943 groups, only 4.

Classified by decade of birth: a fifth of the doctorates held by botanists born before 1870 were obtained in Germany; one fourteenth of those born in the 1870's, but none of those born since 1879. State universities conferred about one fifth of the doctorates on botanists born before 1870, a fourth of those born in the next decade, and nearly a third of those born in the 1880's. Since 1889, however, they have declined progressively in relative yield. Endowed universities conferred about half of the earlier doctorates; but nearly two thirds of those obtained by botanists born in the 1880's, nearly three fourths of those in the 1890's, and five sevenths of those born since. Harvard conferred about half of the doctorates conferred by endowed universities to subsequently starred botanists born before 1860, one sixth of those of

the 1860's, one fourth of those of the 1870's, one eighth of those of the 1880's, somewhat more than one third of those of the 1890's and 1900's. Chicago, Cornell and Hopkins conferred no doctorates on botanists born before 1860, and Columbia only 1. Of the group born in the 1860's, however, Chicago conferred doctorates on 5 (one eighth), Columbia, Cornell and Harvard conferred doctorates on 4, Hopkins on 1. Of the 57 doctorates conferred on the group born in the 1870's, Chicago and Harvard conferred doctorates on 9, Hopkins and Columbia on 5, Cornell on 4. Chicago took a strong leadership for the group born in the 1880's, conferring doctorates on 10 out of the 42; Cornell on 5, Columbia and Harvard 4, Hopkins 2. Of the 33 doctorates to the group born in the 1890's, Harvard led with 9, followed by Cornell 6, Chicago 4 and Hopkins 2. Thus Harvard led as to the oldest and youngest groups, was tied or surpassed by Chicago for the large number born 1860–1889. Cornell tied with Columbia for second place as to those born 1860–1889; took second place for the youngest group. Hopkins tied for third place as to the groups born in the 1870's. Columbia tied for second place for those born in the 1860's, tied for third or fourth place for the next two decades, after which it slumped badly.

Of the 100 botanists starred in 1903, 43 had no doctorate; of the 100 botanists starred 1927–1943, only 9; of the last 50, only 1. Nearly a fourth of the 1903 group had foreign doctorates as did a sixth of those starred in 1909. No native American botanist starred since 1909 has a foreign doctorate. About a fourth of the 1903 group had no graduate work. Almost as many additional (one fifth) had some graduate work but did not receive a doctorate. The percentage of those with graduate study increases progressively until all but 2 of the 25 starred in 1932 had graduate work, and for the 50 starred 1937–1943 all but one.

For their doctorate, most subsequently starred botanists went to a university with an outstanding leader or

group of leaders. The "heads" of the chief departments of botany during much of the period when most of these starred botanists received their doctoral training, 1895–1925, were J. M. Coulter (Chicago), R. A. Harper (Columbia), H. H. Whetzel (Cornell), and at Harvard, a galaxy of successors to Asa Gray.

Zoologists: Fourteen American universities conferred doctorates upon 5 or more subsequently starred zoologists, Bryn Mawr 5, California 5, Chicago 37, Columbia 41, Cornell 16, Harvard 55, Hopkins 38, Illinois 8, Michigan 9, Pennsylvania 11, Princeton 6, Stanford 5, Wisconsin 6, Yale 12. Universities conferring 3 or 4 doctorates are George Washington and Indiana. German universities conferred 26 doctorates, other European universities 4.

In the doctoral training of starred zoologists, Hopkins led as to the group starred in 1903, with Harvard not far behind. Chicago was third with about half as many. For the 1909 group Chicago led; it was second for those of 1921 and 1943. Harvard led for those of 1927 and 1932, was second for 1903 and 1937; Columbia led for 1921 and 1937, was second for 1932, tied for second for 1909. Cornell led for 1943; it tied for second for 1932. For 1927–43 combined (the last 1,000 starred) the totals are Harvard 24, Columbia 16, Chicago 12 and Cornell 12. For 1932–43, Harvard had 16, Columbia and Cornell tied for second with 12. For the most recent groups (1937–1943) Cornell with 8 led, and Columbia and Harvard with 7 tied for second. Chicago and Wisconsin had 5 and Yale 4. Thus it is evident that for each starring, a number of institutions have been close.

The doctoral training of starred zoologists has continuously been predominantly in endowed universities. State universities have conferred doctorates on less than a fourth as many; they stood highest for those born in the 1880's and 1900's, when they conferred doctorates on nearly half as many as did endowed universities. German universities conferred about one sixth of the doctor-

ates to American zoologists born before 1870, to almost no native Americans born since 1880. Hopkins' doctorates were mostly to men born before 1875, Chicago led for those born in the 1870's, Columbia and Harvard tied as to those born in the 1880's, Harvard led for those of the 1890's.

In the doctoral training of subsequently starred zoologists, W. K. Brooks at Hopkins, C. O. Whitman and F. R. Lillie at Chicago, T. H. Morgan at Columbia, L. Agassiz, G. H. Parker, E. B. Wilson and W. M. Wheeler at Harvard, J. H. Comstock and J. G. Needham at Cornell, and R. G. Harrison at Yale merit special mention, although others were highly significant.

Birthplaces

In proportion to the number of immigrants in the United States at about the time of the birth of the starred biologists, Canada and Britain were relatively productive of botanists, while the leaders for zoologists were Switzerland, Austria, Russia and Canada. Switzerland did about five times as well as Germany, reflections perhaps of its small number of immigrants and the influence of Louis Agassiz.

Per million of population at about the median date of the birth of these biologists, New England with 10.6 for botanists and 20.8 for zoologists led. The East North Central States and the Middle Atlantic States were second or third. For both, the South Central States were least productive, less than 4 per cent as productive as New England. By individual states, the yields in proportion to population when they were born was highest for the botanists in Connecticut, Vermont, Nebraska and Michigan. For the zoologists it was the New England States except Rhode Island, with Minnesota and Kansas next.

Where Employed

Of the starred biologists who were not yet aged 66 recently the leading institutions in the number employed

were for the botanists Cornell, California, Harvard, Columbia and Minnesota. For the zoologists the leaders in this respect were Harvard, Chicago, Columbia, Michigan, California and Stanford.

An analysis by decade of their birth indicates that of the younger starred botanists, state universities employ 35, endowed universities 27, U. S. Department of Agriculture 6, colleges only 1, botanical gardens 3. By contrast, of the botanists born before 1880, the U. S. Department of Agriculture employed 27, state universities 45, endowed universities 53, botanical gardens 14 and colleges 4.

Similarly for the zoologists, of the younger groups, state universities employed 24, endowed universities 60, colleges 7, museums, etc., 15. Of those born before 1880, state universities employed 56, endowed universities 92, colleges 20, museums, etc., 29.

QUININE AND CINCHONINE EFFECTS ON GROWTH, DIFFERENTIATION AND LETHAL TEMPERATURE OF DROSOPHILA MELANOGASTER[1]

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In another paper I am advancing an optimum temperature hypothesis for the gene-heat reaction based on 12 vestigial locus genotypes and 96 temperature response curves (Harnly, 1948). The analysis indicates that one is dealing with the synthetic reactions, probably enzymatic, producing wings and affecting other morphological and physiological reactions. This hypothesis is readily open to experimental examination. If one is dealing with an enzyme complex then one should find one or more compounds, known to affect enzymatic processes, that will cause a shift in one or more of the known and measured manifestations of the gene. This attack on the problem has been under way for some time. The experiments on quinine and cinchonine reported here are a part of the work on these other-related and unrelated compounds now being tested in our laboratory. The work reported here supports our optimum temperature hypothesis for the gene-heat reaction of an enzyme complex.

TECHNIQUE

The food used in these experiments was the customary banana agar jell medium containing 10 mg alkaloid/100 cc of food. The proportions used in preparing the food were 50 gr of banana, 2 gr of agar, 40 cc of water and 10 cc of the alkaloid solution. The agar was heated in the water to solution, poured into a heated graduate, and hot water added to replace that lost through evaporation. Then 10 cc of a 100 mg alkaloid/100 cc solution at a pH

[1] This investigation was carried on in conjunction with a project concerning the action of the cinchona alkaloids directed by Dr. Dugald E. S. Brown and under a grant from the Cinchona Products Institute, Inc.

7.2 was added per 40 cc of the water agar solution, combined with the mashed banana and stirred thoroughly. This gave the usual food proportions of 50 gr of banana to 50 cc of water, 2 per cent. agar medium containing 10 mg alkaloid/100 cc food. This was poured into 1- by 4-inch vials to a depth of 25 mm and yeasted 24 hours before the larvae were placed on the food.

Mass matings of *D. melanogaster* laying on trays for 2-hour intervals were used. These trays were incubated at 25° C for 24 hours. Ten newly hatched larvae were picked off the trays and placed on the surface of the food in each vial. These vials were incubated at the temperature indicated. When large numbers of larvae or pupae were needed for the recovery tests 50 newly hatched larvae were placed on the surface of the food in shallow straight walled jars having an inside diameter of 58 mm. The jars were capped with a fine mesh cloth held on by rubber bands.

Recovery of Quinine

(*A*) *Food:* Tests were made to determine whether the quinine placed in the food at the beginning of the experiment was present throughout the entire feeding period or was eliminated by something in the banana, the yeast or the waste products of the larvae. Quinine tests on the control food in which larvae had developed were negative. Tests on the experimental food in which larvae had completed their feeding period showed 10.7 mg quinine/100 cc of food. These results demonstrate that the alkaloid is present in the designated concentration in the food during the entire feeding period. The value determined at the end of this period is slightly higher than the original concentration. This difference is probably due to the loss of water by evaporation from the food during the larval period resulting in a slightly higher concentration of quinine in the food at the end of the period of oral administration.

(*B*) *Pupae 25°* C.: Tests were made for quinine on 500 control and 500 experimental black vestigial-pennant 24-

hour-old pupae. These tests showed no quinine present. The test used would show the presence of free and bound quinine. If the feeding larvae take in the quinine with their food it either passes through the digestive tract without being absorbed or else is in some way eliminated from the tissues of the individual within 24 hours after puparium formation.

(*C*) *Larvae 25° C.:* Larvae are easily and quickly obtained from the surface of the food in straight walled shallow jars if the surface of the food is gently flooded with water to fill all the larval burrows. Under this condition the larvae very quickly come out on the surface of the food and can be picked off with a camel's hair brush or a fine spatula. In the tests for quinine on the black vestigial-pennant larvae precautions were taken to slow down all physiological reactions as the larvae were removed from the food. They were placed in crushed distilled-water-ice in distilled salted water. When the larvae were all picked off the food they were washed twice in crushed distilled-water-ice in distilled water to remove any traces of food and dried on filter paper. Tests were made on 849 control and 938 experimental larvae removed from the food within 3 hours of puparium formation. These tests showed no quinine reaction in the controls and a value of 6.32 mg quinine/liter of larvae. This value demonstrates that the larvae had taken in the drug orally with their food and absorbed significant quantities of it from the digestive tract. Hiatt (1944) has administered orally a dosage of 10 mg quinine/kilogram of body weight to humans and found plasma values that varied from individual to individual between 2.5 and 4.5 mg quinine/liter. A value of 6.32 mg quinine/liter for mature *D. melanogaster* larvae demonstrates that they have absorbed significant quantities of the drug into their body fluid and tissues. But within 24 hours after the animal has stopped feeding the quinine has disappeared from the body. This elimination in the first 24 hours of postpuparial development can not be by excretion since there is no excretion or elimination during the pupal period.

Since the presence of bound quinine is detected by the test used, the quinine present in the body fluid and tissues of the larvae just prior to puparium formation is evidently destroyed by metabolic processes during the next 24 hours, as is the case in vertebrate tissues.

Effects on Growth and Differentiation

In the data reported above the control and experimental larvae tested for quinine were brothers and sisters from eggs laid during the same time intervals. The larvae feeding on the control food reached maturity and puparium formation at the usual time for 25°, but the larvae feeding on the experimental 10 mg quinine/100 cc food medium required 33 per cent. more time to reach maturity and puparium formation. Using weight as a measure of growth the mean weight per 1,000 individuals for the control larvae was 1.23 gr and for the quinine larvae was 1.63 gr at maturity and puparium formation. This is a 33 per cent. increase in the weight of the experimental larvae over the control larvae. It is evident that quinine at this concentration markedly retards differentiation as marked by puparium formation but has no effect on the rate of growth (as measured by weight) since the increased growth (weight) per cent. was equal to the increase in duration of the larval feeding period. Hence the action of quinine in prolonging the larval period is not associated with semi-starvation. Its effect is to delay differentiation. Whether this is an effect of quinine on the general physiological processes of maturation and differentiation of the organism or on the physiological processes in its ring gland affecting puparium formation can not be determined from the data at present available. However, techniques are available for the resolution of this question.

Shift of Gene Controlled Lethal Temperature

The effects of a 10 mg per cent. quinine or cinchonine food medium on mortality at six temperatures are shown in Table 1. The column headed "larval" shows the mortality per 1,000 during the larval period, *i.e.*, those that

failed to form puparia. Similarly, the "pupal" column gives the frequency of death during the pupal period, *i.e.*, the pupae from which adult imagos did not emerge. The column "total" is the ratio per 1,000 larvae introduced into the vials that did not survive to free living adult imagos. It must be remembered that these are preliminary values based on one trial and an average of 290 individuals per degree-alkaloid-genotype. Though not exact mortality values they do indicate the general effect. The lethal temperatures of vg (vestigial), vg^p (vestigial-pennant), and vg^+ (Wild type) have been determined in our earlier temperature experiments. In each case it has been found that enough animals emerge at one temperature to make wing measurements possible and that none

TABLE 1

MORTALITY PER 1,000

°C	10 mg per cent. quinine			10 mg per cent. cinchonine					
	di vg			b vg^p			vg^+		
	larval	pupal	total	larval	pupal	total	larval	pupal	total
16	143	358	450						
25	169	308	425	193	111	283	72	78	144
27				200	156	325	55	99	148
29	110	652	690	275	222	436	164	167	304
30	117	751	780	136	993	993	186	426	532
31	129	974	978	605	1,000	1,000	248	799	849

emerge at a 1° higher interval. Hence the lethal temperature is indicated as just above the last point at which some emerge. The respective lethal temperatures for development on the usual banana medium are: vg^p 30°+, vg 31°+ and vg^+ 32°+. It is evident from Table 1 that both quinine and cinchonine fed in a 10 mg per cent. concentration lower this point 1° for these three alleles, the respective lethal temperatures of the treated animals being vg^p 29°+, vg 30°+ and vg^+ 31°+.

This action of quinine and cinchonine, in lowering the threshold of the lethal effects of extreme heat, proves to be the explanation of the apparent toxic effects of these alkaloids when fed in this concentration. The death rate of di (dimorphos) vg larvae is quite constant between 16° and 31° (table 1). At 16° and 25° the pupal mortality

is constant and double that of the larval stage, at 29° it is sixfold and at 30° sevenfold the larval value, and 31° is lethal. The data indicate: (1) there is no significant temperature-quinine relationship during the feeding period; (2) the major mortality effect of quinine is during the pupal period; and (3) quinine affects the processes of metamorphosis at high temperatures resulting in the death of all pupae where some survival is obtained in the absence of quinine. Quinine was present in a significant concentration in the mature larva. Within 24 hours after puparium formation this quinine had disappeared from the tissues and body fluid as a result of chemical reactions. These physiological changes markedly raised the pupal mortality in the higher temperature range and lowered the threshold 1° for the lethal heat effects on the processes of metamorphosis.

There are several differences from the above in the data in Table 1 for b (black) vg^p and vg^+ reared on a 10 mg per cent. cinchonine medium. In contrast to the di vg data there is no significant difference between the b vg^p larval and pupal death rate at any interval below the lethal temperature, nor is there any rise in the pupal mortality as the lethal temperature is approached. At the lethal point of 30° the entire increase in value is found in the pupal period. The vg^+ data agree with that of the b vg^p genotype in showing no significant difference between the larval and pupal death rate at 25°, 27°, or 29° but the vg^+ genotype differs from the b vg^p and agrees with the di vg genotype in showing a mortality rise with heat increments, especially as the lethal temperature is approached.

When the mortality values in Table 1 are compared with earlier data from animals fed the usual banana medium it becomes evident: (1) that the pupal mortality of the vg genotype is normally about double that of the larvae below the approach to the lethal temperature (equivalent to the values for di vg, Table 1, at 16° and 25°; and at 29° the larval value is 137/1,000 and the pupal value is 380/1,000); (2) approaching the lethal tempera-

ture in the vg control there is a marked increase in pupal mortality unaccompanied by an increase in the larval deaths; (3) that quinine certainly and cinchonine presumably are not affecting mortality in either the larval or pupal stage below the approach to the lethal temperature; (4) that near the lethal temperature there is a marked increase in mortality in the pupal period but no significant change in the larval mortality of the alkaloid fed animals; and (5) quinine and cinchonine lower the lethal temperature 1° for these three alleles.

From the above it is evident that quinine and cinchonine are not, in themselves, toxic when fed in a 10 mg per cent. concentration. These two alkaloids, associated with the alleles at the vestigial locus, lower the threshold 1° for the detrimental effects of extreme heat, the lethal point of vg^{+} being lowered from 32°+ to 31°+, vg from 31°+ to 30°+ and vg^{p} from 30°+ to 29°+. The mortality curves are consequently depressed giving an apparent but unreal direct toxic effect of quinine and cinchonine in the upper reaches of the mortality curves.

Discussion

The data presented demonstrate that certain compounds can be administered orally in the food to *D. melanogaster* larvae, that the drug will be taken in with the food and, depending upon the compound, may be absorbed from the gut into the body fluid and tissues in appreciable amounts. At one stage it can be detected and at a later stage (without any loss through excretion or elimination) no trace of it is found, demonstrating that it must enter into the chemical reactions taking place in the living organism (*i.e.*, metabolized). Two results of these reactions have been reported here.

Quinine definitely retards differentiation, as marked by puparium formation and the onset of metamorphosis, without affecting growth as measured by the increase in body weight. At present it is impossible to state how this effect is brought about. Semi-starvation will retard development. In test cases we have repeatedly placed

parents, *e.g.*, black, in half pint milk bottles and allowed them to lay eggs for part of a nine-day laying period, then removed these black parents and replaced them in the same bottles with Wild type Gray parents for the rest of the nine-day laying period at 25°. This has been followed by an 18-day count from first emergence of the imagos. In no case were any Gray body colored animals obtained, thus proving that the black flies emerging on the 18th day of the count had taken considerably more than 18 days from egg to imago instead of the usual 9 days at 25°. But these animals, retarded by semi-starvation, are markedly smaller than their sibs emerging during the first days of the count in the same bottles. Baumberger (1919) has subjected *D. melanogaster* larvae to starvation and semi-starvation diets. Puparium formation is markedly retarded in his semi-starvation experiments and the animals are correspondingly smaller in size. When semi-starvation retards differentiation as marked by puparium formation growth is likewise affected and the individuals are smaller. Our animals fed on a quinine-containing medium have a 33 per cent. longer larval period, but they increased 33 per cent. in weight above the controls. These facts demonstrate that quinine is not causing semi-starvation and so affecting growth during the larval stage, but it is entering into the larval metabolic processes concerned with differentiation. Since the ring gland produces a pupating hormone one may assume, until further data are available, either that the quinine in the larva is acting on the ring gland, retarding its growth and functional maturity and so delaying puparium formation and metamorphosis, or that it enters into the synthetic processes in the ring gland, or with the ring gland and so delays differentiation. This much is certain, during the larval period quinine fed in this concentration does not affect growth but does affect differentiation.

Quinine fed in this concentration and detectable in a significant quantity in the mature larvae just before puparium formation is not present 24 hours later in the pupa. Quinine certainly and cinchonine presumably enter into the chemical reactions during this period and

have a measurable effect during the pupal period. There is no significant difference between the control and experimental larval and pupal death rates (degree for degree) below the close approach to the lethal temperature. The significant difference is in the lethal point itself. In the case of each allele the threshold for the lethal effects of high temperature during the pupal period has been lowered 1° by the alkaloid. The hypothesis that the vestigial alleles are affecting chemical processes, possibly enzymatic in nature, and that these alleles differ in their optimum temperature and not in their type of reaction (constructive) is based on our 96 temperature response curves of 12 genotypes at the vestigial locus (Harnly, 1948). In the earlier experiments it was shown that the lethal temperature is a characteristic of the allele at the vestigial locus in these genotypes and is allele specific for the vg, vg^p, and vg^+ genes. In the data reported here the two related alkaloids, quinine and cinchonine, have lowered the threshold for the lethal effects of heat and the lethal temperature of each genotype 1°; these drugs are known to affect enzyme reactions, especially in the upper temperature range; and they have shifted clearly and sharply one of the known and measured manifestations of these three alleles. This uniform result for these three genes makes more probable our hypothesis advanced for enzyme action at this locus and these mutations resulting primarily in shifts in the optimum temperature for their reactions.

Summary

(1) The larvae of three vestigial locus alleles were fed food containing either quinine or cinchonine in a concentration of 10 mg/100 cc.

(2) Tests of the food showed quinine present in the desired concentration throughout the feeding period.

(3) Tests of control food, larvae and pupae were negative.

(4) Tests of quinine-fed larvae some three hours before puparium formation gave a value of 6.32 mg quinine/liter.

(5) Tests of quinine fed individuals 24 hours after puparium formation were negative. The quinine in the body fluid and tissues had been metabolized within 24 hours after the animals had stopped feeding.

(6) Sib controls from the same egg-laying period formed puparia at the usual time for 25° C.

(7) Quinine fed individuals had the larval period prolonged 33 per cent. and weighed 33 per cent. more than their control sibs. This alkaloid markedly retarded differentiation but did not affect growth as measured by their weight.

(8) Quinine and cinchonine shift the gene-controlled lethal temperature 1°; vg^{p} from 30°+ to 29°+; vg from 31°+ to 30°+; and vg^{+} from 32°+ to 31°+.

(9) The apparent toxicity at high temperatures of these alkaloids fed in this concentration is actually due to a shift in the gene controlled lethal temperature.

(10) The retardation of differentiation with no effect on growth, the shift in the gene controlled lethal temperature, and the presence of quinine in the body fluid and tissues just prior to the end of the feeding period but its absence 24 hours later all demonstrate that this alkaloid is absorbed from the gut, enters into the metabolic processes of the individual, and furthermore at least one of these processes (lethal temperature) is associated with the activity of the alleles at the vestigial locus.

(11) Quinine and cinchonine are known to affect enzyme reactions, especially in the upper temperature range. The uniform results with these two alkaloids and three vestigial alleles make more probable our hypothesis, advanced elsewhere, for enzyme action at this locus and that these mutations have resulted primarily in shifts in the optimum temperature for their reactions.

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PROGRESS REPORT ON BASIC CLASSIFICATION

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THIS paper presents the results of study of the primary classification of organisms, the system of kingdoms, as continued beyond my previous discussion of the subject (1938). The present contribution was read and discussed at a meeting of the Western Society of Naturalists and again by a group called together by Dr. S. F. Light, of the University of California. The participants on these occasions showed a gratifying interest. I did not receive, and must not convey, the impression that the scheme here put forward was accepted. Cogent criticisms were offered. These are cordially appreciated, and have been applied in revision, in part, according to my own judgment and responsibility.

The conventionally accepted distribution of organisms between two kingdoms, Plantae and Animalia, requires revision as a matter of intellectual consistency. It is generally acknowledged that the boundary between the two kingdoms is indefinite. Two considerable groups, the myxomycetes and the flagellates, are regularly claimed for both kingdoms.

As to the myxomycetes, this situation was produced by the studies of a distinguished botanist. De Bary (1858), having discovered the essential features of the life cycle of these organisms, expressed the opinion "dass die Myxomyceten nicht dem Pflanzenreiche angehören, sondern dass sie *Thiere*, und zwar der Abtheilung der *Rhizopoden* angehörig, sind." He emphasized this opinion by further publication in a zoological journal (1859). The resulting uncertainty is not a serious matter: the myxomycetes are believed to be a derived group whose position does not affect that of others.

On the other hand, the position of the flagellates is recognized by most biologists who are concerned with the

theory of classification to be of critical importance. It appears that either kingdom, maintained in its conventional limits but with the exception that the flagellates are conceded to the other kingdom, would be genetically discontinuous, an artificiality, taxonomically untenable. If the flagellates are plants, the other Protozoa are cut off from the bulk of the animals; if they are animals, various groups of algae and fungi are cut off from the main body of the plant kingdom.

The difficulties described would be avoided by acceptance of the well-known proposal of Haeckel (1866), that all organisms which are not definitely either plants or animals be made a third kingdom under the name of Protista. Haeckel was regrettably ambiguous in his original presentation of these ideas. He entertained the hypothesis of the repeated origin of life, and suggested that each phylum (*Stamm*) might have arisen from lifeless matter independently of all others. If this suggestion were sound, the kingdoms of plants and animals would be inherently artificial, and the separation from them of a group of Protista would be meaningless.

The proposed kingdom Protista was for a few years treated as conceivably sound. Bütschli (1889) assembled the arguments against it. He pointed out the ambiguity just mentioned; repeated the argument of Kent (1880), that a kingdom Protista, so far from eliminating a vague boundary between kingdoms, produces two vague boundaries instead of one; and, as a student both of bacteria and of Protozoa, maintained that these groups are too diverse to be included in a single kingdom. Bütschli's presentation, in an authoritative work, of these and other objections, is apparently responsible for the subsequent consensus of opinion that no additional kingdom is to be recognized. The problem of a definite and natural limitation of kingdoms is not an immediately practical one, and few since Haeckel have attempted to solve it.

The opinion which I have urged against the accepted system is essentially this: that so far as known and living

organisms are concerned, the differences in character by which the primary natural groups can be distinguished have been discovered; it remains only to recognize as kingdoms the groups thus distinguished.

The most profound of all distinctions among organisms is that which separates those without nuclei from those which possess them. The former are the bacteria and blue-green algae. Organisms of this type have presumably been in existence much longer than the nucleate organisms (and we may speculate that they will survive longer in a changing world). They are much more numerous in individuals, but they do not reach considerable complexity of structure nor great variety of type. This comparative lack of differentiation is apparently related to the absence of the nucleus, which makes the precise transmission of a complicated heredity impossible. The organisms thus set apart are evidently to be treated as a kingdom: they are different from plants and animals in greater degree than the latter are different from each other.

The classic authorities for the belief that life originated on earth by natural physical processes (Haeckel, already mentioned, and Lamarck (1809) before him) believed in a repeated origin. The latter idea, however, is not a necessary consequence of the former. Whether or not life originated more than once, it is certain that life possessing nuclei came into existence once only, by evolution from non-nucleate life. This conclusion is as certain as any which can be based on induction: it is established by the uniformity of the nucleus, in its structure and in its behavior, in mitosis, in sexual reproduction, and as the vehicle of Mendelian heredity, wherever it occurs.

In the course of the extensive evolution of nucleate organisms, certain characters or combinations of characters appear to have come into existence only once. Such characters or combinations of characters are useful to the scientist as the marks of natural groups suitable for taxonomic recognition. They are properly used in the formal definition of taxonomic groups, subject to a single qualifi-

cation. Evolution can erase what it has created, and it is proper to classify as members of a group organisms which have by degeneration lost its formal positive characters.

Among groups of nucleate organisms distinguished as just described, two are outstandingly extensive.

One of these is a group of organisms living by photosynthesis, with the further peculiarity that this process takes place in bright green plastids called chloroplasts and containing the four pigments chlorophyll A, chlorophyll B, carotin and xanthophyll, and no others. Whereas living creatures in general, from bacteria to men, store carbohydrate as glycogen, the members of this group produce the specialized carbohydrate starch; and whereas different organisms deposit a wide variety of lifeless hard substances as shells or frameworks, the members of this group produce for these uses an additional specialized carbohydrate, namely, cellulose. This group is the main body of the plant kingdom as conventionally construed, and I have proposed that it be treated exclusively as the plant kingdom. It is an obviously natural group. It may be assumed, for example, that photosynthesis within this group is almost absolutely a uniform process, while in other groups it differs more or less considerably in connection with the presence of additional pigments.

Even more numerous is a group of multicellular predatory organisms, prevalently motile, and with prevalently naked cells. Members of this group are distinctively marked by two stages, the blastula and the gastrula, through which they individually pass in embryonic development. This group makes up the bulk of the animal kingdom as conventionally limited, and may well be treated as constituting exclusively the animal kingdom. Like the plant kingdom as here limited, it is an obviously natural group. It is the realm within which studies of comparative anatomy are pertinent. Embryological resemblances within this group are, in general, matters of homology. Resemblances extending beyond it are matters of analogy; they show the capacity of life to repeat itself, but do not indicate relationship.

The described circumscription of kingdoms respectively of bacteria and blue-green algae, of plants, and of animals, leaves unplaced a miscellany of algae, fungi and protozoa. For nomenclatorial purposes, this miscellany is the same thing as the kingdom Protista of Haeckel. By the proposed sharp limitation of the kingdoms of plants and animals, one of the objections to Protista as a taxonomic group is avoided; the exclusion of the bacteria affords a partial answer to another. Still, the remaining organisms are an unfamiliar assemblage and undeniably heterogeneous. They are, however, a natural group, having genetic continuity by the fact that they include the original form of nucleate life and all of its descendants except those two specialized secondary developments, the familiar kingdoms of plants and animals. They could legitimately be treated as several kingdoms, but it is not possible to present knowledge definitely to delimit these, and several of them would probably turn out to be ludicrously inconsiderable in this rank. The entire assemblage, then, is to be treated as a single kingdom. It is expected that familiarity will make it acceptable.

The system of four kingdoms thus proposed, assuming that it has been shown to be sound in itself, can not come into practical use until it is provided with tenable systems of subsidiary groups and of nomenclature. The purpose of the present contribution is to meet these requirements. As preliminary to this, I attempt a concise statement of the basic postulates of classification, a part of which have been taken for granted in the foregoing discussion.

All who study at all extensively the classification of organisms know that we are dealing with a system which extends backward in time through unnumbered years. Considered in finest detail, this system may in most parts be visualized as a network; it is a network so far as different individual organisms are able to interbreed and produce fertile progeny. Considered otherwise than in fine detail (visualized, that is, upon such a scale that the apparent units are separated by sterility barriers), it is a

branching system resembling a tree. It consists of lines which divide, diverge and redivide, and are incapable of anastomosis.

The system thus described is the natural system of the classification of organisms. Because of that historical revolution by which the Linnaean classes and orders of plants were driven from use, the expression "natural classification" is familiar to botanists. One reads of natural classification as though it were something which a scholar could formulate and publish in a book. The sense in which this expression has been used should evidently be amended. That which is natural exists irrespective of human will or knowledge; it is to be discovered, not formulated or invented. We know much about natural classification in general, and we realize that we can never know it in full detail. Very much of it has perished, and what survives is of an intricacy which has defied extensive detailed knowledge.

The published systems which have inaccurately been called natural are forms of the taxonomic system. By practical and intellectual necessity, man maintains a comprehensive man-made system of classification of organisms, whose function is to serve as a register of, and index to, the entire knowledge of organisms. This is the taxonomic system. Because the taxonomic system serves its function more effectively the more closely it resembles the natural system, and because knowledge of the natural system is constantly advancing, the taxonomic system is subject to constant revision. By the nature of things, and not by human will, it is impossible for any man or body of men to formulate the taxonomic system or any part of it with confidence that further experience will never necessitate revision. One may describe the taxonomic system as a conventionalized representation of the natural system so far as the natural system is known. It is not and can not become identical with the natural system; the two are related as an artist's representation, of a tree for example, is related to an actual tree. Lamarck (1809) stated

definitely the concept that taxonomy, a work of man, is inherently artificial, though guided by nature so far as nature is known.

Three of the conventions of taxonomic classification are conspicuous:

(1) We know that we are dealing with a continuum, but we conceive it as broken into sharply limited fragments. Nature, and our own purpose in carrying out this work of mental disarticulation, place one stringent limitation upon it. So far as we can recognize the natural system, we recognize no taxonomic group which is not genetically continuous within itself. A group which is acceptable under this requirement is legitimately called a natural group. It is not by caprice that we insist that tenable groups be natural: these groups and no others possess a fundamental unity making it worth our while to recognize them.

(2) The groups are assigned to fixed grades called categories (*i.e.,* lists). As an outcome of history, there are seven cardinal categories, those of kingdoms, of phyla or divisions, of classes, of orders, of families, of genera and of species. Every individual (sterile hybrids are sometimes excluded) is assigned to one group of each of these seven kinds. Agassiz (1857) is responsible for this practice: in his opinion, the existence of precisely these seven categories is a fact of nature. We know that he was mistaken. What we call a species is a fragment of a network, limited neither by nature nor merely at random, but by our own convenience, as a suitable unit of classification. The collection of individuals which we call *Canis familiaris* is a markedly different sort of thing from the one we call *Ginkgo biloba.* Similarly, at a somewhat higher level, the groups are parts of a branching system considered separately for purposes of human thought. One may say that because Agassiz took the categories seriously, we accept them as a convention. The international rules of botanical nomenclature prescribe all seven categories. The zoological rules deal only with families,

genera, species, and their subdivisions, but zoologists recognize the other categories in practice.

(3) Each recognized group is named. Basic conventions prescribe the language of scientific names, namely Latin, and their grammatical nature. Names of higher groups are proper nouns (or, and more frequently, adjectives used as nouns) in the plural. Names of genera are proper nouns in the singular. The name of a species consists of two words, a generic name followed by a modifier. By the rule of priority, each group has only one valid name, being the oldest which is tenable. It is not by an additional convention, but as a consequence of the ones just stated, that priority takes its start from the works of Linnaeus in which binomial names were first consistently applied to species.

Names acquire a status—the question of whether or not they have priority is pertinent—upon publication. There has been much controversy as to whether particular names were truly published by their first appearance in print, and it appears that taxonomists may justly insist upon two requirements, (*a*) that the vehicle of publication be such that taxonomists may reasonably be held responsible for knowing that the names exist; and (*b*) that the groups named be so specified that they can be identified.

The comparatively modern invention called the type system is a device for meeting the latter requirement. By it, each group named is specified by a single example, with the effect, that the name is never to be so applied as to exclude this example. This practice is so widely accepted and so useful that it may be regarded as an additional fundamental convention of nomenclature. Experience has demonstrated a need for judgment in the application of it: proposed strict rules as to its operation have occasionally yielded results contrary to common sense.

The principles stated are qualified and modified, in rather profoundly divergent fashions, by the respective systems of rules of nomenclature enacted by international conventions of botanists and zoologists. Both sets of

rules warrant the arbitrary retention, by international agreement, of certain exceptional names.

Here we are to deal with organisms removed from the jurisdiction of both codes. As noted, the codes are not in perfect agreement. As human works, they are not perfect in themselves. It will not be expedient to apply either of them to the range of organisms now under consideration. It remains necessary to apply the basic principles of nomenclature. All of us are convinced devotees of priority; any of us will discard a newer name for an older one, and there is no authority recognizably competent to make exceptions in present cases. It is a matter of experience that the taxonomic proposals of Haeckel lost force, in part, through nomenclatorial caprice. The following qualifications of the fundamental principles appear expedient, and the effort will be made to apply them consistently.

(1) Priority is binding within categories: the valid name of a group is the one first applied in the correct category. The practice of shifting names from one category to another is warranted by the codes, but creates confusion. With exceptions as concession to usage, a name which has been used in more than one category should be applied in that in which it was first published.

(2) Names with the conventional endings, *-ales, -aceae, -idae,* and the like, are used subject to the following qualifications: (*a*) They are to be applied only in the categories in which they are customary. (*b*) So far as they are adjectives, they must be modified in gender if this is necessary to make them agree with the names of the kingdoms under which they are included. (*c*) So far as they imply resemblance to something, they are invalid if not based on names of genera, valid or otherwise, included in them.

(3) The mere plural of a generic name is not tenable as the name of a higher group. This point, stated by de Candolle (1813) is not to my knowledge a feature of any code, but it is a matter of common sense. *Ericae,* used by Jussieu as the name of an order, means the species of

genus *Erica;* it does not mean and cannot designate the genus together with its allies.

(4) The many names which are older than the type system, so far as the groups to which they were originally applied are of more than one subordinate group, are without genuine types. They are to be handled, under the type system, by selecting in each an included group to be treated as a type. The group so selected may be called a type, or more accurately a standard (Sprague, 1926); it differs from a genuine type in being selected as a matter of judgment, and in remaining open to argument. The type or standard of each group should be as specific as possible: the type of an order is not necessarily a family: it were better a species, and better yet a specimen preserved in a museum.

(5) Certain venerable names originated as designations of heterogeneous assemblages within which no types or standards can be recognized. The botanical rules call such names *nomina ambigua* and warrant their abandonment. The license thus admitted is necessary, but it is to be exercised with the utmost diffidence.

The effect of the foregoing considerations is to define the work of the taxonomist. Dealing successively with greater or smaller assemblages of organisms, he has first of all the duty of deciding whether each is natural. Provided a group is natural, he has to decide upon the category in which it will most satisfactorily be placed. In the third place, he must decide, by research largely of an antiquarian nature, what is its valid name. Taxonomic work is inevitably of a speculative and literary character; it does not belong to the primary body of science, but is a legitimate secondary development. We maintain that it is worthy of respect because it is practically and intellectually useful. For example, a system of classification may guide physiologists investigating the distribution among organisms of immediately practical physiological characters.

Practically, taxonomic work is performed in satisfac-

tory fashion, and commands acquiescence, in the degree that the author possesses an intimate knowledge, both original and literary, of the organisms with which he is dealing. Deficiency in literary knowledge produces the recurrent grave annoyance, that groups are discovered to have older names than the familiar ones. To this annoyance we are inescapably bound to submit: the aforementioned device, of arbitrary retention of names by international agreement, is a dangerous palliative, which weakens the system of nomenclature every time it is applied. I am personally embarrassed by the fact that the names which I formerly used for the two additional kingdoms now appear untenable: the embarrassment is increased by the fact that Stanier and van Niel (1941) have used one of these names on my authority. No man, none perhaps since Lamarck, has been qualified to deal authoritatively with the entire known range of life. The propositions here put forward are authoritative in form, as required by convention, but they are not authoritative in spirit. They represent the best present knowledge and opinion of one individual, here submitted to the biological community.

Kingdom 1. Mychota Enderlein Bakt. Cyclog. 236. 1925. The organisms without nuclei, bacteria and blue-green algae.

Haeckel (1866) applied the name Moneres to a phylum (*Stamm*) of Protista defined by lack of nuclei, and I (1938) applied this name, in the form of Monera, to the present kingdom. Further study of Haeckel's original publication makes it clear that the standard example, the presumptive type, of Moneres, is the genus *Protamoeba*. *Protamoeba* is an amoeba without a nucleus: Schaeffer (1926) has explained it as a broken-off fragment of an amoeba. At any event, it does not exist as an organism, and the name typified by it is not applicable to anything.

On a subsequent occasion, Haeckel (1894) published a kingdom Protophyta. It consisted of the blue-green algae together with a part of the green algae; it was an outright

artificiality. The name had been used by Endlicher (1836–1840) in two different senses in the same work. Zoologists have occasionally referred to Protophyta as though it were a taxonomic group of plants; but the botanist is unable to identify the group intended. The name is in fact incapable of definite application, and to be rejected as a *nomen ambiguum.*

The fact that the name Mychota, here applied, originated in a notoriously heterodox system is not under any nomenclatorial code a valid objection to it. It can (and must) be replaced only if some other name, having a type within the group, is found previously to have been applied to it explicitly as a kingdom.

Phylum 1. Schizophyta (Cohn) Wettstein Handb. Syst. Bot. 1: 56. 1901. Schizophyta Cohn 1875, without definite category. Phylum Archephyta Haeckel 1894, non Haeckel 1866. Phylum Archezoa Haeckel 1894, non Perty 1852.

It seems expedient to treat the entire kingdom as a single phylum. There are at least three profoundly different groups within it: the proper bacteria, the myxobacteria and spirochaets, and the blue-green algae. Most of the sulfur and iron bacteria appear to be related to the blue-green algae. The groups are not highly numerous and varied, and if we make a phylum of each we will be bothered with numerous phyla of a single class or classes of a single order.

Kingdom 2. Protoctista Hogg in Edinburgh New Philos. Jour. n. s. 12: 223. 1861. Nucleate organisms other than plants and animals.

This is the same group as Protista Haeckel Gen. Morph. 1: 203. 1866. Bütschli, in his searching criticism of Haeckel's proposal, pointed out several earlier proposals to the same effect. The name *Psychodières* Bory for the additional kingdom is not tenable as not being in Latin form. Owen (1860) applied to it the familiar name Protozoa; this may be rejected in this usage because it had previously been applied to a class and to a phylum. The

name here cited, published as a substitute for it, is next in order of time.

Phylum 1. Rhodophyta Wettstein Handb. Syst. Bot. 1: 183. 1901. Phylum Rhodophyceae Engler Syllabus ed. 3: 18. 1903. The red algae are here treated as including the most primitive of nucleate organisms, according to the suggestion of Tilden (1933). The obvious characters of most members of the group do not suggest this action. The higher red algae possess perfectly typical nuclei; certain peculiarities of their reproductive processes are evidently matters of specialization. The nuclei of most of the lower red algae (Bangiales), as described by Dangeard (1927), are of the utmost simplicity in structure and behavior, as though primitive; they are nevertheless in all respects genuine nuclei. There remains the genus *Porphyridium,* which has been classified sometimes as a red, sometimes as a green, and sometimes as a blue-green alga. The account of its cytology by Lewis and Zirkle (1920) includes puzzling features which may perhaps be interpreted as follows. A large central plastid, in which stainable rods appear, is the homologue of the central body of the blue-green algae. A minute separate body which breaks up into fragments during cell division represents a stage in the evolutionary origin of the nucleus.

Phylum 2. Protoplasta Haeckel Gen. Morph. 2: xxiv. 1866. Under this heading most of the flagellates are to be included. Since many other groups are evidently descended from organisms treated here; and since the unicellular character, the presence of flagella, and the function photosynthesis occur both among Mychota and among the flagellates; the latter have been regarded as including the most primitive nucleate organisms. A closer study of the chrysomonads (apparently the most primitive group within that of flagellates) casts doubt on this idea. Cells of chrysomonads are prevalently without walls; in connection with this structural feature, the group exhibits a widespread tendency to holozoic nutrition. These characters are evidently not primitive. Furthermore, the fla-

gella of flagellates are much larger and more complicated than those of bacteria. It seems probable that they are not homologous structures in the two groups, but independently evolved.

A paper of Luther (1899) contributed significantly to understanding of the classification of the flagellates. The ordinary green algae, as typical plants, produce starch and cellulose. They reproduce by zoospores bearing paired equal flagella. The flagellates called phytomonads or Volvocales are of the same character; so definitely so, that in our effort to represent nature, we necessarily classify them as green algae and valid plants. There are some few aberrant green algae which do not produce starch and cellulose, and whose zoospores bear paired unlike flagella. Luther noted the existence of certain flagellates of like character, related to the aberrant green algae as the Volvocales are related to the typical ones. He named the group which he had thus recognized as a class, Heterokontae. His discovery conveys two ideas: that relationships among the flagellates are recognizable by pattern of flagella and by metabolic products; and that different groups of flagellates have given rise to parallel series of derived groups.

These ideas were applied by Pascher (1914), who demonstrated a close relationship between the chrysomonads, the Heterokontae, and the diatoms. He named the combined group as a phylum, Chrysophyta. In the groups mentioned, and in other groups of flagellates, he demonstrated the repeated parallel evolution of amoeboid organisms. Subsequently (1921) he showed that the colorless flagellates of family Monadina Ehrenberg (Monadidae or Monadaceae of later authors) belong to the group of chrysomonads.

Different flagellates differ significantly in the detailed structure of the flagella. Loeffler (1889), in his original publication of the standard method of staining the flagella of bacteria, remarked that he had incidentally applied this method to certain larger organisms. He found the fla-

gella of *Monas* to bear numerous lateral appendages, and the cilia of a certain infusorian to bear solitary terminal appendages. Loeffler's method is difficult, and it has not been very extensively used. Fischer (1894) used it and coined terms, *Flimmergeisseln* and *Peitschengeisseln,* designating structures of the respective types seen by Loeffler. Petersen (1929), having applied Loeffler's stain to a reasonable variety of flagellates, introduced a refinement of terminology. Flagella of the type of the larger flagellum of *Monas* (the organism bears also a minute simple flagellum) became *allseitswendige Flimmergeisseln.* Those of *Euglena,* which bear a single file of appendages, became *einseitswendige Flimmergeisseln.*

Deflandre (1934) devised a different method of seeing the appendages on flagella, and substituted, for the Germanisms just quoted, French terms based on Greek. These may be Anglicized as follows.

(1) The acroneme flagellum bears a single terminal appendage (Fig. 1). The flagellum without appendages is said to be simple; so far as it appears among flagellates, it appears to be a variant of the acroneme type. Acroneme and simple flagella are the only ones known among Volvocales, *Bodo,* and the polymastigote flagellates. In all these groups, the flagella are borne at the anterior ends of the cells.

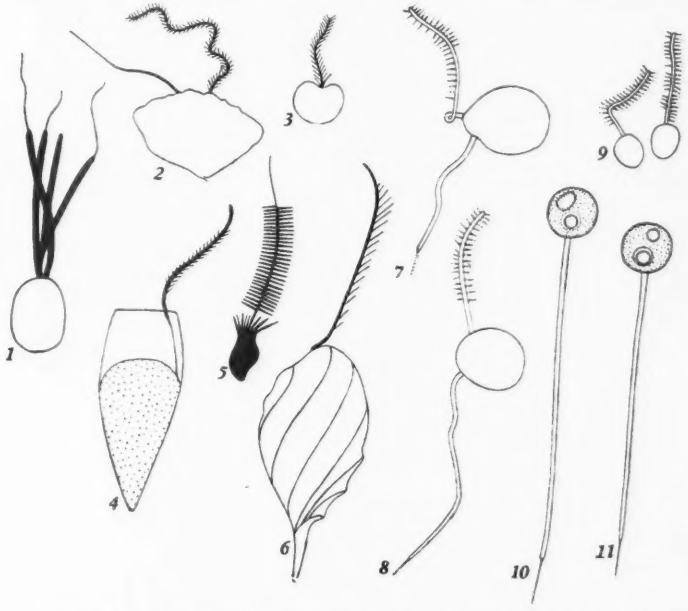
(2) The pantoneme flagellum bears appendages on all sides (Figs. 2, 3, 4). Among chrysomonads and Heterokontae, each motile cell bears one pantoneme flagellum, usually with an additional acroneme one. This is true of organisms such as *Synura* (Fig. 2), in which the two flagella have been supposed to be alike.

(3) The Choanoflagellata bear flagella with both lateral and terminal appendages (Fig. 5). These are called pantacroneme, and are perhaps a variant of the pantoneme type.

(4) The stichoneme flagellum bears a single row of appendages (Fig. 6). It is well known to occur in *Euglena,* and Deflandre found the lateral flagellum of *Glenodinium* to be of this character.

These observations are to be compared with those which Couch (1941) made upon the zoospores of lower fungi. The latter structures are of three types:

(1) In the typical Oomycetes, the water molds and downy mildews, each zoospore bears one pantoneme flagellum and one acroneme one (Figs. 7, 8). It is clear that these organisms are immediate allies of chrysomonads of



FIGS. 1–6. Flagellates, stained by Loeffler's method, after Petersen (1929). 1. *Carteria* sp. 2. *Synura uvella*. 3. *Monas obliqua*. 4. *Dinobryon sertularia*. 5. *Salpingoeca* sp. 6. *Phacus pyrum*. FIGS. 7–11. Zoospores of aquatic fungi, after Couch (1941). 7. *Saprolegnia ferax*. 8. *Achlya caroliniana*. 9. *Rhizidiomyces apophysatus*. 10. *Siphonochytridium* sp. 11. *Rhizophidium carpophilum*. All × 1000.

the type of *Ochromonas* and *Synura*, but the group is so extensive as to require separate taxonomic treatment.

(2) The small group of aberrant chytrids of family Hyphochytriacea, of which Karling (1943) has made a distinct order, produce zoospores with a solitary anterior

pantoneme flagellum (Fig. 9). This group is evidently related to chrysomonads of the type of *Chromulina* and *Dinobryon*.

(3) All typical chytrids, and the Monoblepharidalea and Blastocladialea, produce zoospores with a single *posterior* acroneme flagellum (Figs. 10, 11). The relationships of this group remain obscure.

Ellison (1945) has examined the zoospores of certain typical myxomycetes and of *Plasmodiophora*. The flagella are acroneme (or simple, or sometimes knobbed at the ends); usually solitary in typical myxomycetes, paired and unequal in *Plasmodiophora*.

The effect of these observations is to confirm the existence of several markedly distinct types of flagellates and the more or less parallel evolution from them of several other types of organisms. It is impossible to present knowledge to state confidently the natural classification of all these groups; particularly, it is impossible to place most of the rhizopods. It appears expedient to set up a taxonomic group including, (1) all flagellates except those which are known to lead directly into other major groups (specifically, the Volvocales, which belong with the plants); and (2) all the minor groups directly descended from them. The resulting group will be a miscellany, but it will be preferred to a large number of doubtfully natural groups of high taxonomic rank. This group will be a phylum. The oldest names for distinct phyla for the accommodation of the organisms here considered were published by Haeckel in the *Generelle Morphologie*. Rejecting the first of these, Moneres, for reasons already given, we apply the second, Protoplasta, of which the evident type or standard is *Amiba* Bory (Haeckel used, of course, the conventional mis-spelling *Amoeba*). The following classes are recognizable:

Class 1. Heterokontae Luther in Bihang svenska vetensk.-Akad. Handl. 24, afd. III, no. 13: 19. 1899. Class Chrysophyceae Pascher, 1914. Chrysomonads, proper Heterokontae, Monadina, Hyphochytriacea, and,

tentatively at least, the Choanoflagellata. Organisms whose motile stages bear one pantoneme or pantacroneme flagellum, and, usually, an additional acroneme one.

Class 2. Diatomea Haeckel Syst. Phylog. 1: 91. 1894. Although rarely or never producing flagella, the diatoms are known to be immediate allies of the chrysomonads. The group is distinct, numerous, and varied enough to be treated as a separate class.

Class 3. Oomycetes Winter in Rabenhorst Kryptog.-Fl. Deutschland 1, Abt. 1: 32. 1884. The group is to be limited to organisms producing motile cells bearing one pantoneme and one acroneme flagellum. These organisms are also evident immediate allies of the chrysomonads.

Class 4. Zoomastigoda Calkins Biol. Prot. 253. 1926. Non-pigmented flagellates with exclusively acroneme flagella. The Bodonidae, Polymastigida and Hypermastigida; presumably also the Rhizoflagellata and Plasmodiophoralea. The group is questionably natural.

Class 5. Myxogastres (Fries) Engler and Prantl Nat. Pflanzenfam. II, Teil, p. 1. 1889. The typical myxomycetes, their relationships being presumably with the Rhizoflagellata.

Class 6. Archimycetes A. Fischer. The typical chytrids and their allies, producing zoospores with solitary posterior acroneme flagella.

Class 7. Flagellata (Cohn) Kent Man. Inf. 1: 27, 211. 1880. This name, originally published (1853) without definite statement of category as a new name for the order Astoma of Siebold, Phytozoidea of Perty, was obviously a later synonym when applied to an order by Claparède and Lachmann (1858). It will be simplest to treat it as rendered valid by Kent's use of it in the category of classes. Bütschli (1883) applied to the same class Diesing's subordinal name Mastigophora; the latter has been widely used. Cohn's reference to Astoma Siebold fixes *Astasia* as the standard example. Whatever class includes this genus must bear this name (or an earlier one); and whatever order includes it must be called Astoma.

Pascher combined the cryptomonads and dinoflagellates in one group. The observation of Deflandre, already mentioned, links the dinoflagellates with the euglenids, and Chaufeaud (1936) assembled all three, and also the chloromonads, but failed to apply a scientific name: he called the organisms in question *protistes trichocystifères ou progastréades*. The group appears to be natural; it appears to be satisfactorily ranked as a class; and it includes the standard example of class Flagellata.

Class 8. Rhizopoda Siebold in Siebold and Stannius Lehrb. vergl. Anat. 1: 3. 1848. The amoeboid organisms have repeatedly been shown not to be a natural group. It is proposed, accordingly, that those few whose relationships are apparent be placed accordingly; that three major natural groups (the myxomycetes, already listed as a class, and two groups listed below as phyla) be set apart; and that the remainder be allowed to stand as here, as an acknowledgedly artificial group appended to the flagellates.

The remaining phyla of Protoctista include organisms which are of great interest both practically and as examples of what life can produce. They are believed to have evolved independently of one another from the Protoplasta, and to have led to nothing further: they do not command interest as supposed evolutionary links between one group and another. A brief enumeration of them will be sufficient for present purposes.

Phylum 3. Phaeophyta Wettstein Handb. syst. Bot. 1: 171. 1901.

Phylum 4. Inophyta Haeckel Gen. Morph. 2: xxxvi. 1866. The higher fungi together, at least tentatively, with the Zygomycetes.

Phylum 5 is to include the Foraminifera; it has apparently never been named as a phylum.

Phylum 6 is to include the Heliozoa and Radiolaria, and is likewise as yet unnamed as a phylum.

Phylum 7. Fungilli Haeckel Syst. Phylog. 1: 90. 1894. This is the oldest name for Sporozoa as a phylum. The

group is manifestly artificial, and to be maintained only tentatively.

Phylum 8 is to include the ciliate organisms. It offers a nice problem in nomenclature. The phylar name Protozoa Siebold had originally been applied to a class; possibly Archezoa Perty could legitimately be taken up. There are two classes, Protozoa Goldfuss, 1824 (Infusoria Siebold, 1848), and another whose valid name I have not determined, the oldest name as such, Acinetae Haeckel, being the mere plural of a generic name.

The kingdom Plantae, having been duly limited, requires no further discussion.

Regarding the kingdom Animalia, reference should be made to Dubosecq and Tuzet (1937), who have substantiated the place of the sponges in this kingdom. Owen included the sponges in kingdom Protozoa, and Haeckel included them in the original publication of Protista. Later, Haeckel studied and reported upon the reproduction of sponges and concluded that they are animals. Subsequent observations revealed grave errors in his account, and led to the belief that the cell-layers of embryonic sponges are not homologous with the extoderm and endoderm of typical animals. The detailed observations of Dubosecq and Tuzet show this belief to be mistaken. The sponges produce true blastulae and gastrulae, ectoderm and endoderm. Furthermore, their processes of spermatogenesis and oogenesis are of typically animal character.

The widely entertained hypothesis which was first put forward by James-Clark (1866, 1868), that the sponges are derived from the Choanoflagellata, continues to appear tenable. It appears probable that the animal kingdom evolved directly from the chrysomonad group, and not, as has been suggested, from the *Progastréades* of Chaufeaud, the proper class Flagellata as here construed.

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FAMILY MERIT AND INDIVIDUAL MERIT AS BASES FOR SELECTION. PART II

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INBREEDING AND FAMILY SELECTION

Inbreeding can change the effectiveness of family selection in two ways. First, it can make r higher than is possible without inbreeding. Second, it can alter the size of the three kinds of variance, A, C and E, thus making some additional changes in t. The effect on r is much the more important. As long as there is no inbreeding, r can not exceed .50. If maternal sibs are also avoided, in order to prevent a C term from maternal environment, r can not rise much above .31.

How closely r depends on inbreeding is illustrated by the following examples. In a population of unselected inbred lines, r between full sibs equals .5 $\left\{1+\frac{F+F'}{1+F}\right\}$ where F is Wright's inbreeding coefficient for the sibs and F′ is the inbreeding of their parents. Between paternal half sibs r equals .25 $\left\{1+\frac{3F+F'}{1+F}\right\}$ where the three parents are equally inbred and equally related to each other. Inbreeding thus makes it possible to build families in which r is high, although the members are not maternal sibs. For example, in a large one-sire herd closed to outside blood r will reach .39 in the first inbred generation, .50 in the second and .58 in the third.

Also inbreeding can make n large without lowering r. In species which are not very prolific, such as cattle and sheep, it is difficult without inbreeding to get enough members to make the family average dependable. By inbreeding it is possible to hold the family together (*i.e.*, to keep r at about its initial level) until it has members enough to make $\frac{(1-r)A+E}{n}$ small and thus to permit the

family average to declare the family's breeding worth rather accurately. This can be important when t is small; *i.e.*, when E is large and C is small.

Inbreeding may alter slightly the ratios of A and C and E to each other by shifting epistatic or dominance variance from E to C or A. Changes in these ratios do not change r directly but they may change t. Since $t = \frac{rA + C}{A + C + E}$, it is apparent that increases in C will raise t, while increases in E will lower it. Increases in A would lower t if $(1-r)C > rE$, but would raise it if $rE > (1-r)C$. Inbreeding will increase A linearly with $1 + F$ if there is no dominance or epistasis, but with some curvilinearity if those are important.

Thus the general effect of inbreeding is to make family selection much more effective in a population of partially inbred but unrelated lines than in the random bred population from which they were derived. Most of this comes simply from increasing r or (in the less prolific species) from making n large without diluting r.

However, selection *between* the families will lead to discarding the poorer families as soon as they are definitely known to be such. This will decrease A and r, markedly. Then the effectiveness of further selection between families will be much lower until such time as the selected families can be intercrossed and the crosses interbred to permit recombinations which would release again the potential genetic variability which is within a population of selected inbred but unrelated lines.

The practical usefulness of inbreeding merely to make family selection more effective is limited because of the time required to inbreed the lines. This makes it impossible to harvest in every generation the benefits of selecting between inbred lines. For example, two generations of inbreeding in a one-sire line are necessary to raise r to .50. Then at least one more generation will be needed for crossing two or more selected families. Another generation is needed for interbreeding the hybrids to permit

gene recombinations and still another to form families of half sibs around the good individuals among those segregates before the inbreeding can be resumed and the cycle repeated. This complete cycle requires at least five generations. In only one of these could the full benefits of selection between such distinct families be reaped.

The fact that individual selection can be practiced in every generation might permit the total progress due to individual selection during a complete cycle of inbreeding to be considerably larger than the more spectacular progress which family selection would make in the one generation in which it could be so successful. These considerations weigh against instituting an inbreeding program *solely* to reap the benefits of family selection; yet certainly if inbreeding is already under way for other reasons, appropriate use of it will enhance the effectiveness of family selection.

Family Selection for All-or-None Characteristics

Some characteristics can be measured in individuals only by an all-or-none classification, even though the differences between the individual breeding values form a continuous distribution. An important example is disease resistance. Usually it is not feasible to classify the individuals into more than two classes—those which die and those which survive—even though those which died differed widely in their resistance and those which survived differed widely in how close they came to dying. This limitation on the accuracy of measuring individual phenotypes is much less severe on family averages. The individual must go in one or the other of only two mortality classes, but the average mortality in a family of n can take any one of $n + 1$ values, equally spaced from zero to 100 per cent.

The effect of this coarseness of grouping is to increase E and is enough by itself to make t small for nearly all characteristics which have only a two-way phenotypic classification. Since r is unaffected, this lowering of t

automatically makes family and combination selection considerably more effective for such characteristics than it would be if individual phenotypes could be measured on a continuous scale. This appears to have been included adequately in the preceding formulas and curves.

Family selection also has the advantage that it can increase markedly the intensity of selection for characteristics having an all-or-none classification, particularly when the frequency of the undesired class is low. For example, suppose that in a flock of chickens the mortality during the first year in the laying house is 30 per cent. but that only 40 per cent. need to be kept for a second year. If only mass selection were practiced, the 40 needed out of each 70 survivors would have to be chosen at random, as far as mortality is concerned. If family is considered, the 30 to be culled out of each 70 survivors will be those from the families which had the highest average mortality. For undesirable characteristics which are not quite lethal, such as cross beaks in chickens or crooked legs in swine, one even has the option of keeping for breeding some of the few defective individuals which occur in the families with the very lowest percentages of such defects. That is not true of pre-reproductive mortality, since natural selection does there all the individual selection for mortality which can be done and the breeder's only option is how much further he will go with family selection.

Qualifications and Special Conditions

For simplicity certain complications have been neglected in the preceding pages. These are mostly of minor importance and will not often alter the main conclusions but they will be mentioned briefly.

(1) Except where the family is a set of full sibs, the various members are not likely all to be equally related to each other. For example, if all the offspring of a sire or dam are considered as a family, as when poultry breeders speak of a sire family, most of these will be half

sib to each other but a few will be in sets of full sibs and perhaps several will be three-quarter sib to each other. Such heterogeneity of the family will still leave the preceding conclusions approximately valid if for r is used the average of the r's within such a family.

(2) The phenotypes of the various members of the family may not all be equally well known. For example, a cow may have a full sister who already has three records while she herself has but one, and she may have another sister who has not yet freshened. Those animals whose phenotypes are most accurately known should receive more weight than the others in the family average. But the extra attention which should be given to the most thoroughly tested ones is often nearly balanced by the lesser attention which should be given to the ones with the less certainly known phenotypes. The net result on Y and t is much the same as if each were known with the average degree of accuracy. The proper emphasis on the family average will vary from one individual to another according to the completeness or accuracy with which the phenotype of that individual is known. In terms of equation (5) this is to say that $\frac{A}{A+C+E}$ is larger for P–Y than it is for Y–$\overline{P}$. The importance of this will depend on how much larger r_{GP} actually is when P is an average of several observations, or otherwise known with unusual accuracy, than when P is a single observation or even an incomplete observation, such as a heifer's production during only the first three months of her lactation.

(3) In the actual use of a selection index it is always possible that the values used for r and t may not have been quite correct. Selecting on a combination of family and individuality therefore will often be a little less superior to the other two methods of selecting than has been indicated here. This discrepancy will be small, since the correlation between P and Y will cause which-

ever one of them is over-emphasized to pick up part of the load which should have been carried by the other.

(4) Some families may be related to each other. This has the effect of lowering r when making selections between individuals belonging to these families. In such cases the effective r between members of the same family is $\frac{r_2 - r_1}{1 - r_1}$ where r_2 is the relationship of the members of the same family to each other and r_1 is the relationship of members of one family to members of the other family. This lowers the usefulness of the family average for selecting between related groups. For example, when selecting entirely within the progeny of one sire, the effective r between full sibs is only about .25 to .33 (depending upon the relationship between the dams of the various sets of full sibs) instead of .50. The common sense of this is obvious when one considers the extreme case of selecting between full sibs, in which case the family average is useless. When selecting between half sibs, the parent which they have in common partly determines the merit of both sets of full sibs. Thus that part of r which derives from the common parent serves no useful purpose in discriminating between two half sibs.

(5) The distribution of phenotypes may be distinctly skewed, while the distribution of family averages will be more nearly normal. If more than half of the individuals can be culled and if the long tail of the P distribution is toward low merit, as would be the case if most causes of low merit are individually rare defects, the family average will be somewhat more useful than indicated here. If the long tail of the P distribution is toward high merit and if less than half can be culled, the family average will be a bit less useful, relative to mass selection, than has been indicated by those formulas.

(6) Would the relative effectiveness of the three methods be the same in subsequent generations? Only under rare combinations of genetic conditions would changes in heritability be large within as short a time as four to six

generations. Whatever the direction of this change, the method of selection which changes the mean most rapidly will also produce the largest changes in A and hence in t. Thus it appears that the preceding conclusions may usually be extrapolated for at least three or four generations without much error.

(7) Dominance and epistasis have been mentioned only casually. The variance caused by them is mostly in the E term, but a little of it is in C. Even if dominance and epistasis are important the conclusions concerning general breeding value are scarcely affected, especially when r is small or moderate. But when each family is a highly inbred line, little if at all related to the others with which it is being compared, dominance and epistasis will swing the balance farther in favor of family selection, especially for special breeding values (Sprague and Tatum, 1942). This may have been the major way in which the improvement in hybrid corn was wrought; *i.e.*, by using inbreeding to make r high enough that selection for special breeding values could be effective.

(8) A negative correlation between the environments of family members has the same effect as if C in the preceding formulas were negative. Some tendency to such a negative correlation could arise if the average environments of all the various families were forced to be nearly identical without, however, reducing the environmental variation within families. For example, if all litters are given exactly the same limited number of pounds of feed per pig but within each litter the litter mates are free to compete with each other for that limited amount, then the average consumption of feed per pig will be forced to be the same for all litters, but within each litter some pigs will get more and others less than the average amount. Or, if season of hatching makes a pronounced difference in the characteristic being measured in chickens, then hatching different families in different seasons or times would contribute a strong seasonal effect to C. But if all families are hatched rather uniformly through-

out the same long period, then the seasonal differences will contribute considerably more to the intra-family variance than to the differences between family averages. Peck-order and other social dominance phenomena within families reared together could conceivably have a noticeable effect of this kind.

Such balancing of environmental differences between families without eliminating them within families lowers C, and hence t. This lowering of t will naturally make the family average more useful than if such balancing were not practiced. The formulas seem to describe that correctly.

(9) For some characteristics selection must be practiced before the individual is old enough to manifest its own phenotype. An example is selecting for longevity. Or perhaps measuring its phenotype requires destroying it, as is the case with many carcass characteristics in animals and with most chemical analyses of seeds in plants. Or the characteristic may be incapable of expression in one sex, as is butterfat production. In all such cases where the individual's own phenotype is known only dimly or not at all but other members of its family have had their phenotypes observed, family selection is relatively more important than has been indicated here, simply because the individual's own phenotype is not available for use.

Only the seventh and ninth among these qualifications seem likely often to modify the general conclusions importantly. To the extent that they are important, family selection will be more effective, as compared with mass selection, than has been indicated here. The seventh can hardly be important except in populations in which r is large and from which the families and individuals with low general combining ability have already been culled. The ninth is merely the truism that, when the phenotype of the individual being selected is known less accurately than the phenotypes of its relatives, the effec-

tiveness of mass selection is lowered more than that of family selection.

Implications for Man

In the many choices which must be made between one human being and another the question often arises as to how much attention should be paid to the family of each; *i.e.*, to the reputation and accomplishments of his close relatives, to his social or professional class, to the schools he attended, to his racial descent, etc.

The main difference between this and the problems of animal and plant breeding is that in choosing between human beings we are usually interested in the future

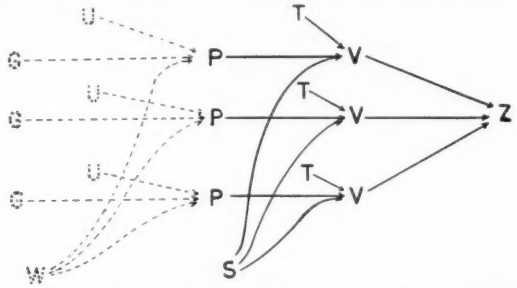

Fig. 12. Path coefficient diagram of biometric relations involved in predicting phenotypic performance (P) in man from some test or indicator (V). The dotted parts show how this is an extension of the problem of predicting breeding values.

phenotypic performance of the individual, rather than in the quality of its offspring. For example, we are chiefly interested in future performance when we elect a congressman, choose a foreman, hire a stenographer or appoint a professor.

Fig. 12 shows the biometric relations involved. The solid lines show those which are pertinent for predicting the future performance (P) from an indicator (V).[5] The

[5] This is drawn, as if P, the desired characteristic or performance, were a cause of V, the indicator. Actually P is not yet observable when the choice must be made. It is more plausible to consider P and V both to be caused partly by intrinsic ability, K, already unfolded to the extent of

dotted lines are not pertinent here, but show, in the same terms as the plant and animal breeding case, how the correlation between the P's of members of the same group may be partly environmental through W and partly genetic through similarity of the G's. To make the preceding formulas valid while still using the same symbols, only two changes need to be made in the definitions: Let r_{PP} now be r and r_{VV} now be t. As before, t consists of two parts. One comes through r_{PV} and r and makes the group average (Z) helpful positively in predicting an individual P. The other comes through things (represented by S) which act directly on the indicators to make them tend all to be high or all to be low for the same group, but do not affect the P's. This portion of r_{VV} which comes through S makes Z useful negatively as a means of correcting partially for the effects S has had

expressing itself in V but not yet in P. Then it is r_{KK} rather than r_{PP} which should be used in place of r in the earlier formulas. But r_{KK} can not be observed directly. It will be identical with r_{PP} if P is determined wholly by K; will be larger than r_{PP} if the subsequent environmental impacts which make P different from K are random as between family members; but could be smaller than r_{PP} if things subsequent to K which modify P strongly are highly correlated. The second of these alternatives seems likely to be true most frequently, but doubtless that would vary with the characteristic and especially with the basis of the grouping. When r_{KK} does exceed r_{PP}, the group average should receive more positive attention than is indicated here, where r_{KK} and r_{PP} are considered to be equal.

A general solution with no assumptions at all concerning the causal relations between P and V may be had by letting $r_{PV} = a$ and the correlation between the P for one member of the group and the V for another member equal b. Then the equation for predicting P from its own V and from Z, the average of the V's for that group, turns out to be:

$$P-\overline{P} = \frac{\sigma P}{\sigma V}\left[\frac{a-b}{1-t}(V-\overline{V}) + \frac{(b-at)}{1-t}\cdot\frac{n}{1+(n-1)t}(Z-\overline{Z})\right] \qquad (6)$$

The denominators are exactly the same as they were in equation (4), keeping in mind that t now refers to V, rather than to P. The numerators are also the same if b equals ra, which is the case pictured in Fig. 12. In any event, a, b and t can be measured directly in any sample of data in which P and V have both been observed on two or more members each from many groups. If the sample was sufficiently large to make the fiducial limits on a, b and t usably small, and if the observer is sure enough that the sample is really representative of the population on which he wishes to use it, he ran use equation (6) directly.

on the V for the individual whose P is being predicted. V can be a variety of things, such as an intelligence test, school grades, civil service rating, letters of recommendation, general reputation, etc.

If the criterion for judging what we want of the individual is highly accurate and can be applied directly to him, then almost nothing is gained by considering the characteristics of the group to which he belongs. This corresponds to the plant and animal breeding case in which heritability of individual differences is high and mass selection by itself is almost the perfect method of selection.

But often the criterion from which individual merit is estimated is far from being perfectly accurate and many mistakes will be made when it alone is used. Also many decisions, such as the kind of education or vocational training or apprenticeship a person should have, must be made while he is still too young for his tendencies and capabilities to be appraised as accurately in him as they could be later. Yet his parents, aunts, uncles and some other close relatives or members of the same group may have reached the age when appraisal of their abilities in this field is most accurate. Whenever the correlation between actual individual merit and whatever criterion is used for estimating it is moderate or low, there is a chance to make the choices more accurate by giving some attention to the individual's close relatives or to the average characteristics of his group.

As a concrete example, suppose students are grouped according to the high school from which they came and we wish to select those who will make the best grades in physics at college, as if we were awarding a limited number of scholarships intended to increase the number of well-trained physicists. Suppose further (without committing ourselves as to whether it is a good guide!) that we select these students according to their high school grades in Latin. Then college grade in physics is P and high school grade in Latin is V in the symbols of

Fig. 12. The high school attended is the basis of grouping and the average grade in Latin for students at that high school is Z. If there is no correlation between V and P, that is equivalent to saying that $\frac{A}{A+C+E}$ in our earlier notation is zero and therefore that prediction on this basis will achieve nothing. If the high schools differ genuinely in the effectiveness with which they prepare their students to do good work in college physics, or if they draw their students from families or populations which are distinctly unequal in their abilities to do the kind of work required in college physics, then r will be a real quantity. To the extent that this is so and high-school Latin grades are correlated with college physics grades, we should give some preference to students from high schools where the average grade in Latin is high.

But if the high schools differ widely from each other in their standards of grading Latin, then t will have a large term from S in addition to whatever t may or may not have from r_{PP}. In this example of high-school grades, the probability of S being a considerable term is so well recognized that grades from different schools are almost universally compared in terms of quartiles or other expressions of V–Z, with no attention at all to Z–$\overline{V}$, except perhaps when those making the decisions may know personally something about the average college performance of students who have come from these different high schools in the past. But r is not likely always to be the zero which would entirely justify deciding on V–Z alone. Among other kinds of groupings than high school attended, and for other characteristics r will sometimes be large enough and t small enough to warrant giving the group average considerable positive instead of negative attention.

If some schools prepare their students expressly to pass certain tests, such as a civil service examination, by drilling them on sets of questions from previous tests of that kind, while others educate them in a more general

way in the fundamentals of the duties they are likely to perform, then it is easy to see how t in the ratings on such tests could be very high for students from the same school and yet those making the appointments should give negative attention to Z and make the choices mostly on V–Z, rather than on V–$\overline{V}$ which is what they do if no attention is paid to school.

The idea that each individual should be judged on his own characteristics alone, regardless of what or who his relatives or associates may be, has a strong sentimental appeal to our sense of justice and fair play. Yet justice and fair play for the employer whom the foreman will serve, or for the students whom the teacher will teach, or for the patients whom the doctor will treat, also demand that no pertinent information which would lead to the choice of the abler persons for these tasks should be neglected.

The question reduces to the factual one of how best to use such pertinent evidence without over-using it. Where r and t are practically equal, little is gained by considering the characteristics of the group; as good a job of selection can be done by considering only the individual's own indicator. But where r and t are widely different a better job can be done if the group average receives proper attention. Actual measurement of r and t in human populations is not difficult if the data are available.[6] The r and t merely describe how much more the group means differ from each other than they would if all the groups were just different random samples from the same population; r pertaining to the characteristic which is really wanted, and t pertaining to the indicator, or compound of several indicators, from which that characteristic has to be estimated at the time the choices are made.

Environmental factors which tend to be alike for members of the same group but to vary from group to group

[6] Except for determining the r_{KK} mention in footnote 5, when that is likely to be different enough from r_{PP} to need separate determination.

and which affect the desired characteristic strongly (*i.e.*, W in Fig. 12) will tend to make r high but they will have less effect on t unless they affect the indicator directly in other ways. An example is home environment prevailing during early childhood, if those home precepts and examples affect mature conduct importantly and if each group is a set of full sibs. Also the early-taught codes of conduct vary at least a little between social classes, economic strata, professions, religions, students at different schools, groups based on separate cultural or racial origins, etc.

Environment which affects the indicator directly but does not affect the desired characteristic will raise t if that environment tends to be alike for members of the same group (*i.e.*, S in Fig. 12) but will lower t if that environment (T in Fig. 12) is as likely to be different between members of the same group as it is between members of different groups.

Where the basis of grouping is primarily genetic, as when it is race or consanguinity, and when it is partially confounded with genetic differences, as when it is childhood environment, cultural index of the home, etc., r is likely to exceed t. Then the individual's future performance is likely to be more correctly estimated if, in addition to its own individual rating, it is given some extra credit for belonging to a good group and is given some penalty for belonging to a poor group. Biologists work usually with such groupings; that is, with groupings whose r and t values properly place them toward the left corner of Figs. 9 and 10.

Where the basis of grouping is primarily economic or sociological or geographical, except sometimes when the latter is also confounded with racial differences, t is likely to exceed r and the case properly belongs toward the right corner of Figs. 9 and 10. Sociologists and economists naturally are more likely to be working with groupings of this kind where the individual should be penalized for being in a good group and should be given extra credit for

being in a poor group. To some extent this justifies the philosophy of *noblesse oblige* and of being more lenient with the man from "the wrong side of the tracks."

The word "corner" unfortunately bears rather too apt an analogy with prize-ring terminology. The biologist and the social worker often come out fighting with each other on these matters! Some of that diversity of outlook and at times acrimonious controversy might fade away if it were clearly understood that there *are* four corners to Figs. 9 and 10 and that for one characteristic one of these corners may be correct, while for another characteristic or another grouping another corner or some intermediate location may be correct.

Much of the heat which often enlivens or embitters those controversies is generated by the second of the fallacies described so clearly by Jennings (1930, pages 208–9); namely by attributing solely to one cause what is really due to many causes. For example, in the animal and plant breeding cases it will have been noted that the numerator of t is $rA + C$. A real value for t can result either from the first term, which is the genetic one, *or* from the second term, which is the environmental one, *or* from both of them in varying proportions. Even a perfect demonstration that C is a real term in a given case does not prove that the rA term is zero unless C of itself is measured so exactly that it is known to account for *all* of t. As examples consider the recent controversies in *Science* (101: 16–17 and 200; 102: 86; 104: 231–2; and many previous ones) about interpreting undisputed differences in mean performance of certain racial groups. In terms of the present article, these writers all agree that t is real; the argument is over whether *any* of this is due to an rA term or *all* of it comes from C. Some who are strongly impressed by the evidence that C is a real part of t argue as if they supposed that proof of the reality of C was automatically proof that rA must be zero! An example of a frank recognition that *both* parts of t may be real and of an apparently unbiased attempt

to measure them is Dr. Burks's study (1938) of mean differences in I.Q. between occupational classes. She found the ratio of C to the rA term to be 34:66 in the Stanford data and 23:77 in the Minneapolis data.

Conclusions

(1) The increases in the population mean which are expected to result from one generation of mass selection, or of purely family selection, or of the best combination of the two, are in the following ratio, mass selection being used as a standard:

$$\text{Mass selection} \qquad 1$$

$$\text{Purely family selection:} \quad \frac{1+(n-1)r}{\sqrt{n[1+(n-1)t]}}$$

$$\text{Combination selection:} \quad \sqrt{1+\frac{(r-t)^2}{1-t}\cdot\frac{n-1}{1+(n-1)t}}$$

These are shown graphically in Figs. 9 and 10 for the cases $n = 5$ and $n = 21$. Figs. 3 to 8 show special aspects of these comparisons. In these formulas r is the intraclass correlation between breeding values of members of the same family, t is the intraclass correlation between their phenotypes, and n is the number of individuals in the family.

(2) Under all conditions the combination is at least equal to the other methods, but at some values of r and t its superiority is hardly enough to make the extra computations worth while. The combination is most superior to the others under either of two sets of conditions: (1) when r is moderate and t is much smaller but yet well above zero; and (2) when t is distinctly larger than r.

(3) Mass selection is more effective than purely family selection except when t is less than $r^2-\frac{(1-r)^2}{n}$. Mass selection is as effective as combination selection when r and t are equal and almost as effective unless the difference between them is at least as large as .10.

(4) Purely family selection is almost as effective as the combination selection when r is extremely high and t is low. Also mass and combination selection are not

available, but family selection may be, when selecting for sex-limited characteristics in the sex which can not show them, or for carcass or other characteristics which can not be measured without destroying the individual, or for such characteristics as longevity which have not yet expressed themselves at the time when the choices must be made.

(5) Paradoxical though it may seem, family selection is most helpful and most needed for characteristics in which members of the family resemble each other least; *i.e.*, when t is small. When family members resemble each other closely and families are therefore conspicuously distinct from each other, either the characteristic is so highly heritable that individual selection is not needed, or each family is affected so strongly by its own special environment that the phenotypic average of the family is but slightly correlated with its average breeding value.

(6) Making n large increases the effectiveness of family selection and of combination selection markedly only when t is extremely small and r is very large. At other combinations of r and t most of the benefits of having the families large are already harvested by the time n is as large as 4 or 5.

(8) When t exceeds r the family average plays a negative part in the combination selection. The family average is then more useful as an indicator of inter-family environmental differences, for which its proper use automatically makes partial correction, than as an indicator of the probable breeding value of the individual. To use the family average negatively is to judge the individual largely by its deviation from the average of its family.

(9) Inbreeding will increase the effectiveness of family and combination selection markedly, mainly by increasing r. But this large gain can be harvested only once in each cycle of inbreeding, selecting and crossing the best families, and then interbreeding the crosses to start new families.

(10) Qualifications or special circumstances which may occasionally alter the general solution are discussed. The only ones which seem likely to be important at times are: (a) For special breeding values, which dominance and epistasis may cause an individual to have in some crosses but not in others, family selection is more important than indicated here when r is as high as in populations of inbred lines, but this difference is slight when r is as small as .5. (b) Practical circumstances sometimes dictate that some of the culling be done before the family averages are ready for use, or in the sex which can not show a sex-limited characteristic, or for a characteristic which can be measured only by destroying the individual and for which mass selection is therefore not available.

(11) The same general solution applies to man for determining the optimum emphasis on the individual's own qualities as compared with the average qualities of his family, race, social or occupational class, etc. In most choices between one human being and another, the thing being predicted is the individual's own future phenotypic performance, rather than the merit of his or her offspring. That makes r become the intra-class correlation between the phenotypic performance of members of a group for the characteristic in question, while t becomes the intra-class correlation for the indicator from which their future performance is predicted.

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REVIEWS AND COMMENTS

EDITED BY PROFESSOR CARL L. HUBBS

In these reviews and notices of current biological publications emphasis is given to books and major articles which fall within the special scope of THE AMERICAN NATURALIST, in that they deal with the factors of organic evolution. REVIEWS AND COMMENTS are meant to include also such general discussions, reports, news items and announcements as may be of wide interest to students of evolution. Except as indicated, all items are prepared by Dr. Carl L. Hubbs, Scripps Institution of Oceanography, University of California, La Jolla, California. All opinions are those of the reviewer.

Apes, Giants and Man. By FRANZ WEIDENREICH. Chicago: University of Chicago Press, 1946: 1–122, figs. 1–90. $2.50.

IN his Hitchcock lectures at the University of California at Berkeley, a leading student of human evolution reiterates and in some ways modifies and expands his ideas. He recognizes racial differences but rather sidesteps the question as to whether such differences include mental traits. Notwithstanding racial differentiation, "man is a unit when considered as an organism." In his effort to maintain man as a unit and in contrasting the evolutionary lines of apes and men, he repeatedly suppresses evidence of intermediate characters in fossil men. "Not only the living forms of mankind but also the past forms—at least those whose remains have been discovered—must be included in the same species." Despite this view he continues to recognize several genera and now goes so far as to divide the single species into three subfamilies, named Archanthropinae, Paleoanthropinae and Neanthropinae, in most flagrant disregard of logic as well as of nomenclatorial rules. He insists that human evolution is a single line and that "there is not one detail which does not fit in the line and which could, therefore, be excluded from the ancestry of modern man." He admits a fossil man with apelike skull and human chin but peremptorily discards, as not fitting into his uniform scheme of human evolution, the Piltdown man with

human skull cap and apelike jaws. Perhaps he does not know that such differential admixtures of characters are common in speciation. He unconvincingly traces human origin to the *Dryopithecus* stem "in the Miocene or not very long afterward." He pictures human evolution as a lattice, in which progressive evolution within continents forms the vertical lines, "specialization" forms the horizontal lines, and the known kinds of fossil man form the nodes—a novel and logic-racking evolutionary concept. In this diagram, in line with the very tenuously supported concept that man passed through an early phase of giantism, he places *Pithecanthropus erectus* between the giants and more modern "dwarfish" types, though later in the text he puts *Pithecanthropus* on the line between a small ancient ancestor and the giants. He does not distinguish clearly between constitutional types and races, for he adopts an essentially morphological concept of races with little regard to reproductive structure. He suggests the possibility of "92,780 different racial groups" of man, because the 2,560 kinds of blood may all occur in each of the "thirty-eight anthropologically distinct races." Very obviously, clear, modern biological concepts and viewpoints are needed in anthropology.

Charles Darwin and the Voyage of the Beagle. Edited with an Introduction by Nora Barlow. New York: Philosophical Library, 1946: vii + 1–279, frontisp., pls. 1–15, 1 chart. $3.75.

In part by an orienting introduction and occasional critical notes, but chiefly by presenting his own letters (many previously unpublished) and often crude field notes, Charles Darwin's granddaughter lets us see how a frail and reticent youth grew into the most influential biologist of all time, how the revolutionary concept of evolution was born and gradually developed in his master mind. The material pertains to the epochal voyage of the *Beagle*, for Darwin rightly said that this trip "has

been by far the most important event in my life, and has determined my whole career." We marvel at his inquiring mind and at his acumen, for instance in recognizing from a reconnaissance the recency of the uplift of the Andes.

As Lady Barlow explains, "throughout the pages of the note-books there is the closest scrutiny of significant facts, the clearest recognition of unsolved problems, accompanied by an imaginative faculty on a grand scale. His whole being was moved profoundly by the magnitude and magnificence of the problem. . . .Undoubtedly the habit of these years when he pondered continuously on the geological riddles, involving such vast eras of time, framed his mind aright for consideration of the biological problem of species with which geological facts are so interwoven. Fossil marine shells, fossilized bones and teeth of mammals, petrified trees—all these were clues in the great detective story; and all led the way for a direct consideration of species problems as viewed by one brought up on the creationist assumption."

An Introduction to Mathematical Genetics. By LANCELOT HOGBEN. New York: W. W. Norton, 1946: i–xii, 1–260, illustr. $5.00.—Although fairly comprehensive in regard to the analysis of simple gene actions, this treatise is defective in that it does not cover gene systems. Furthermore, the valuable and widely used chi-square test is neglected and no attention is given to Fisher's treatment of selection or to Wright's work on population genetics. For these reasons the book is inadequate for a student of evolutionary genetics.

Human Embryology. By BRADLEY M. PATTEN. Philadelphia and Toronto: The Blakiston Co., 1946: i–xv, 1–776, figs. 1–446 (53 col.). $7.00.—As a lucid, magnificently illustrated account of the development of the human body from gametogenesis to birth and as an integrated part of the complex training of a modern physician, this long

and eagerly awaited book leaves little to be desired. To make room for an adequate treatment of the subject from these points of view, however, little consideration was given to the comparative and theoretical aspects of human embryology. Only occasionally is the phylogenetic basis of a structure given, and then only briefly. "Evolution" is not even listed in the index. Developmental abnormalities are frequently stressed, as the individual organs are successively treated. There is an extended bibliography. This fine volume is touchingly dedicated to the author's distinguished father, William Patten of Dartmouth.

Functional Anatomy of the Mammal. A Guide to the Dissection of the Cat and an Introduction to the Structural Relationship between the Cat and Man. By W. James Leach. New York and London: McGraw-Hill Book Co., 1946: i–viii, 1–231, 96 figs. $2.50.—In view of the plethora of manuals on comparative anatomy we have wondered whether anything new might appear in anatomical instruction. Now we do have a variance in approach —an introduction to a knowledge of mammalian and particularly of human anatomy through a study of the system of the cat, consistently tied in by comparative statements with the conditions in man (to facilitate the comparison, the belly of the cat is called "anterior," its head end "superior," etc.). The approach is not wholly new, for it follows the lead long ago established in a rigid course by Reighard at the University of Michigan, with the well-known text by Reighard and Jennings. In comparison, Leach's approach and text may be described as a curtailment and simplification, with a more functional viewpoint and with the human comparisons more explicit. Evolutionary considerations are largely confined to a few remarks under "The Principle of Homology," in which, despite the functional approach, homology is regarded as referring only to structuring similarity. Four

types of homology are recognized: phylogenetic, serial, sexual and radial. By radial homology the author refers to resemblances within one member of a serially homologous appendage, as within one hand.

Mammals of California. By LLOYD GLENN INGLES. Stanford University Press, 1947: i–xix, 1–258, figs. 1–57, frontisp. + pls. 1–42. $4.00.—Indicative of its scope and limitations is the statement in the preface that: "This book has been written for the student, for the aspiring naturalist, and for all others who want a better acquaintance with and knowledge of the interesting mammals of California. It is intended as an educational contribution rather than as one to scientific mammalogy." Small maps show the ranges in the state and keys give the distinguishing characters of the species and of some subspecies of the land mammals (the sea mammals are weakly treated), but the text furnishes natural history information only for selected species. These accounts, however, are well written and beautifully illustrated.

The California Ground Squirrel. A Record of Observations Made on the Hastings Natural History Reservation. By JEAN M. LINSDALE. Berkeley and Los Angeles: University of California Press, 1946: i–xi, 1–475, figs. 1–140, frontisp., 1 map. $5.00.—One of the ablest of our naturalists contributes this extensive biography of a mammal. Over a seven-year period almost every conceivable aspect of its life was investigated, in so far as favorable conditions permitted. Yet, to illustrate the diversity of information that might be gathered on an animal, I find no mention of the two items of ground squirrel behavior and relations to man that have most interested me, namely, the predominant role of these animals in cliff and canyon erosion and their contribution to physiography and archeology, through the stone types and the artifacts that they dig up. Control is not treated in detail,

but much information that would be basic to sound control is presented. Particularly striking is the evidence on the rapid decrease of the population as the Reservation recovered from the effects of agriculture.

Alaska's Animals and Fishes. By FRANK DUFRESNE. New York: A. S. Barnes and Co., 1946: i–xvi, 1–297, frontisp., figs. 1–92. $5.00.—The author's writing skill and sense of human interest and his intimate knowledge of Alaskan wildlife reflect his long experience as newspaper man and as administrative secretary of the Alaska Game Commission. Lack of technical training is mirrored in the use of "animals" to mean mammals, in the absence of an index, and in the generalities that pervade the species accounts. But let it be understood: there is included a wealth of intimate natural history information, much of it original, from "our last frontier."

The Birds of North and Middle America. . . . Commenced by the late ROBERT RIDGWAY, continued by HERBERT FRIEDMAN. Bull. U. S. Nat. Mus., 50, pt. 10, 1946: i–xii, 1–484, figs. 1–28. $1.25.—The continuation of this highly authoritative treatment of North American birds is a gratification to ornithologists and to naturalists in general. Part X deals with the Galliformes. As in previous parts the treatment consists chiefly of systematic keys, long descriptions of the genera and higher groups, and, for each species and subspecies, an extended account of the color of the sexes at different ages, conventional measurements in millimeters, statement of geographical range (often so cluttered with localities as to be hardly readable), indication of type locality, and a complete synonymy. Eggs, nests, behavior, habitat and other attributes that mean much more to the bird and often to the ornithologist are left to other treatises, which, however, are referred to in the annotated synonymies. Critical remarks on synonymy, systematic interpretation, intergra-

dation and the like are few and are confined to footnotes. We imagine that these seeming defects have been perpetuated for the sake of consistency, though we suspect that the methods of systematic ornithology have been overly systematized and unduly crystallized.

Field Book of Eastern Birds. By LEON AUGUSTUS HAUSMAN. New York: G. P. Putnam's Sons, 1946: i–xvi, 1–659, many figs., col. pls. 1–6. $3.50.—Like most of Putnam's Nature Field Books, this one is well designed for field use by nature lovers and amateur naturalists. The artificial keys and the brief descriptions as well as the "field marks" and the abundant illustrations are based on the appearance of the live bird. Emphasis is also given to characteristic habits, notes and habitat. Ranges are stated in detail. For species that are divided into subspecies, the full account is given for the northern or the wide-spread subspecies, whether or not nomenclatorially typical, and the additional subspecies are treated comparatively, with a clear statement of range.

Birds of the Philippines. By JEAN DELACOUR and ERNST MAYR. New York: The Macmillan Co., 1946: i–xv, 1–309, 1 map, figs. 1–69. $3.75.—Although published too late to be used by the armed services in the field of war, this book should prove valuable to resident and visiting naturalists, as well as to systematic ornithologists. It is essentially a field guide, with very brief descriptions and often remarks on habits and habitats. In systematic treatment, as expected, the authors have combined many genera and have treated many local forms as subspecies rather than as full species. In uniting genera they have exercised their right to opinion, but in classing within one species distinct local forms that are not known to intergrade they may often be replacing evidence with authority, or, as Mayr would say, with inference. The bird fauna of the Philippines, with the exception of the Palawan group, is regarded as a subregion of the Orien-

tal region, and in turn as being divisible into an eastern province, or central or Visayan province, and 3 marginal districts. The Palawan fauna is regarded as a province of the Malaysian subregion, though it is recognized as combining Malaysian and Philippine elements.

An Illustrated Manual of Pacific Coast Trees. By HOWARD E. MCMINN and EVELYN MAINO. With lists of trees recommended for various uses on the Pacific Coast by H. W. SHEPHERD. 2nd ed. Berkeley: University of California Press, 1946: i–xii, 1–409, col. frontisp., figs. 1–415, 2 maps (end-papers). $4.00.—The new edition keeps this manual available to botanist, gardener and layman. It covers about 400 introduced species as well as all the 146 native kinds of the Pacific Coast states and British Columbia. Most of the species are illustrated by clear-cut sketches of diagnostic parts; the palms, only, by photographs of the whole trees. Besides the usual features of a good manual, there is included a 16-page section on "The Origin and Distribution of Pacific Coast Trees." The flora decreases in richness and particularly in endemism toward the north. The migrational and climatic factors in the population of the area are considered. Sources of origin are the boreal regions, the arid Southwest and northern Mexico, the Great Basin and Rocky Mountain regions. Nearly half of the trees are endemic. Many of these are peculiar to the Upper Sonoran Life Zone of California and constitute a part of the "California element," which is isolated by barriers from the Eastern forests. The local distributions are considered in terms of Life Zones, emphasizing temperature as a prime factor. The origin and adaptability of introduced species is also treated.

Wonders of the Great Barrier Reef. By T. C. ROUGHLEY. New York: Charles Scribner's Sons, 1947: i–xiii, 1–282, frontisp. + pls. 1–50 (36 col.). $5.00.—The first American edition makes this superb book available to American

naturalists. The magnificent color plates have been remade with high fidelity directly from the author's Lumière autochrome slides, which, though taken years ago, are seldom approached by the best products of modern color photography. By text as well as by plates the author vividly pictures that wonderland of tropical nature, the Great Barrier Reef of Australia, 1,250 miles of coral, where color runs riot and life flourishes in almost inconceivable variety. The author intended his book for the layman, but every naturalist will profit from its reading and will want it on his shelves, or likely, on his table. There is much information on the habits as well as the appearance of the reef animals; much sound observation, as on the flight of flying fishes; interesting sidelights on the ethnology of the aborigines; throughout, commentaries on the adaptation of the reef organisms to life in an aquatic world of great richness.

Geomorphology. An Introduction to the Study of Landforms. 4th ed., revised. By C. A. Cotton. New York: John Wiley & Sons [1947]: xii + 1–505, frontisp., figs. 1–473. $6.00.—Although illustrated, with a few outstanding exceptions, by New Zealand examples, this treatise provides a comprehensive explanatory description of landforms and as such should prove of value to ecologists, zoogeographers and workers on speciation, as well as to students of geology and geography.

Glacial Geology and the Pleistocene Epoch. By Richard Foster Flint. New York: John Wiley and Sons (London: Chapman and Hall), 1947: i–xviii, 1–589, figs. 1–88, pls. 1–6. $6.00.—Frank emphasis on the phenomena of glaciation limits the value of this book to biogeographers, ecologists, paleontologists, anthropologists and other naturalists on whose researches and interpretations Pleistocene geology has a vital bearing. It will, however, prove to be a source book of considerable value. It does deal, briefly and with moderate documentation, with the

extent of the successive continental glaciations; with Preglacial, Glacial and Postglacial drainages; with Pluvial waters; with Pleistocene chronology; with change in land and sea levels (in which respect the author takes a very conservative stand), and with climatic changes induced by glaciation. It treats even more briefly the fossil record and human history in Eurasia and in the Americas (but not in Africa). The author concludes: "It is now established that man has inhabited America for at least 20,000 years and possibly for 40,000 to 60,000 [*sic*] years." The general treatment is critical, in places perhaps too critical.

Elements of Soil Conservation. By HUGH HAMMOND BENNETT. New York and London: McGraw-Hill Book Co., 1947: i–x, 1–406, figs. 1–114. $3.20.—Where he speaks, the militant crusader of the Soil Conservation Service backs up his remarks by graphic illustrations, convincing statistics and practical suggestions for preventive or remedial action. His remarks are comprehensively organized and are presented simply and clearly. The subject is one of vital importance to all who are concerned with land management.

The Fungi. By FREDERICK A. WOLF AND FREDERICK T. WOLF. New York: John Wiley and Sons, Inc., 1947: Vol. 1, i–x, 1–438, 1 pl., 153 figs. $6.00; Vol. 2, i–xii, 1–538, 1 pl., 82 figs. $6.50.

IN this two-volume treatment of the fungi the authors have attempted "to stress the activities of fungi with a minimum of consideration for taxonomic aspects." They also state that "a conscious effort has been made to deemphasize phylogeny." The result is therefore a considerable departure from the usual treatment of the subject.

Volume I deals with developmental morphology and taxonomy, with emphasis on morphology. Following brief chapters concerning history, culture technique and general taxonomic considerations, there are chapters con-

cerning the major groups, Myxomycetes, Phycomycetes, Ascomycetes and Deuteromycetes. The principal families of each are discussed. Keys are given to the orders and for some of the orders, keys to the families are included. Each taxonomic group is followed by a list of the literature cited.

Volume II covers a number of subjects, with emphasis upon the functioning of fungi. Nutrition, enzymes, respiration and biochemistry are the subjects of the first four chapters. Discussions of the effects of temperature, radiation and substrates follow. Spore distribution, mechanisms facilitating dissemination and spore germination are discussed. One chapter is devoted to genetics and another to poisonous and edible fungi. The interactions of fungi are treated under the heading of associative effects. Fungi as plant parasites are discussed in chapters concerning host penetration, physiologic specialization and plant pathology. The roles played by insects in the propagation and reproduction of fungi and as vectors of plant pathogens are described and a brief discussion of fungous parasites of insects is included. A chapter is devoted to medical mycology. The last four chapters cover geographic distribution, soil fungi, marine fungi and fossil fungi. Each chapter is followed by the literature cited.

These volumes are an important addition to the literature on fungi. They furnish a compendium of information and a valuable reference source. Unfortunately the authors have not always been critical in their selection of literature. It is true that, as they state, it is impossible to consider each subject monographically, but a more extensive and discriminating coverage would have increased the usefulness for the student interested in pursuing the subject farther. Since previous books on fungi have been concerned mostly with morphology and taxonomy, all students of fungi will specially welcome the summary of the literature on functioning of fungi of Volume II.—E. B. Mains.

Le Farfalle Diurne d'Italia. By Ruggero Verity. Florence, Italy: Casa Editrice Marzocco, S. A. Volume I, General considerations and superfamily Hesperides, Dec. 20, 1940: i–xxxiv, 1–131, frontisp., col. pls. 1–4, pls. 1–2, 11 figs.

Volume II, division Lycaenida, July 15, 1943: i–xii, 1–401, col. pls. 5–19, pls. 3–9, 16 figs.—This primarily taxonomic work on Italian butterflies which was published during the war and has just been received, deserves mention here because of the completeness and the magnitude of the work which the author has begun. Dr. Verity is a "medico-chirurgo" whose hobby is the study of geographical variation in butterflies. He is a foremost European lepidopterist whose papers have been published in many European entomological journals. The fine quality of the colored plates is a tribute to a disturbed civilization; to my knowledge the equal of these plates has never been produced in America. For those who are interested in geographical variation, these volumes contain a mine of original information. It is to be hoped that Dr. Verity some day will generalize upon his detailed data. The lack of distributional maps is a serious deficiency in a work dealing fundamentally with and emphasizing geographical variability in populations.—William Hovanitz.

SHORTER ARTICLES AND DISCUSSION

REPRODUCTIVE ACTIVITIES OF DECAPOD CRUSTACEA

EXAMINATION as an integrated whole of the sequence of reproductive events in the shrimp, *Palaemonetes vulgaris* (Say), has cast new light upon several of the classical problems of carcinology. A brief summary of the investigation is as follows:

(1) *Courtship and Sperm-transfer:* In *Palaemonetes,* males respond only to females which have molted to breeding-form but are not yet long-mated or spawned. Females molting from breeding to non-breeding form are not attractive. After once cooperating in copulation, the female resists further courtship, but continues attractive for some twenty minutes. If mating has been prevented, the female continues attractive until spawning (three to seven hours after attractiveness would have ended, had mating been permitted immediately after the female's reproductive molt). From this combination of circumstances, it is evident that there exists a temporary recognition-mark, independent of acquiescent behavior, which either ceases to be produced by the breeding-form female after mating or spawning, or is neutralized at the appropriate time. Since recognition of attractiveness by the male occurs upon contact of his antennae with (apparently) any surface of the female, but does not occur without physical contact, the recognition-mark would appear to be a non-diffusible coating of the integument of the female. Although the superficial events of Palaemonid mating are well known (Nouvel and Nouvel, 1937; Höglund, 1943), their significance seems not to have been realized, and no other critical demonstration that recognition of a nubile female by the male decapod depends upon a special mating signal seems to be known (*cf.* Broekhuysen, 1936, 1937). The suggestion of a chemical mating signal in *Pandalus* by Needler (1931) is based upon a questionable interpretation of male behavior as sexual attraction from a distance without physical contact.

The spermatophore of *Palaemonetes,* which is pinched off at the time of extrusion from a continuous column in the vas deferens, will adhere to any part of the integument of either sex with which it comes into contact as it is extruded; but becomes non-adhesive almost immediately after exposure. It

therefore seems probable that the spermatophores are applied to the female directly from the male genital apertures, without intermediacy of supposed copulatory appendages.

(2) *Formation of the Egg-membranes:* All components of the egg-shell are produced by the ovum or the embryo. No chorion can be detected in ovarian eggs of *Palaemonetes* within the intact follicle. The *first* membrane is developed by the ovum upon contact with a foreign medium (as by oviposition or teasing the ovary in sea-water), and is apparently identical in extracted ripe ovarian eggs with that in those spawned naturally. For a period of about fifteen minutes, beginning twenty minutes to half an hour after spawning or extraction, this membrane becomes capable of fusing with itself or that of other eggs of the same stage. It slowly develops resistance to cold concentrated HCl (dissolving instantly in newly laid or extracted eggs; taking a minute to dissolve after twelve hours, whether in eggs extracted and isolated or those carried normally by the female; and taking twelve hours to dissolve after several days of attachment), but it is always highly vulnerable to KOH. The *second* membrane is developed about half an hour after the first, in eggs extracted or laid, fertilized or not. It becomes closely applied although not cemented to the outer membrane, but does not take part in formation of the egg-stalks. It is insoluble in HCl but soluble in hot KOH. The *third* membrane appears only in fertile eggs, in late segmentation stages about twelve hours after spawning, both in eggs carried by the female and those removed soon after attachment and maintained thereafter *in vitro*. It immediately becomes cemented to the second membrane in a small area located over the future anterior pleonic tergites of the embryo. It is resistant to both HCl and KOH; as is the *fourth* and last membrane produced, which is an embryonic molt-skin with protozoeal appendages.

The egg-shells of a large variety of decapods of all groups prove on careful dissection to comprise three elements, and it may be presumed that this basic character is universal. No previous accounting of the number and derivation of the decapod egg-membranes seems wholly correct, and the most recent detailed consideration (Yonge, 1937) is seriously at fault, although correct in its denial that a membrane exists in the follicular egg.

(3) *Release of Spermatozoa:* The sperm-bearing matrix, which forms the core of the relatively simple spermatophores of *Palaemonetes,* dissolves about half an hour or less before spawning,

in spermatophores attached in the normal area on the female genital sternites, whether spawning occurs one hour or seven hours after sperm-transfer. Spermatophores misplaced elsewhere about the female during struggles after the first copulation persist undissolved until picked off in fragments by the chelae of the female, sometimes remaining until after spawning. Intact spermatophores on the genital sternite are never plucked off, but the sperm-free cortex, which remains undissolved, is removed after spawning. It is evident that a substance serving to free the sperm-cells is released by the female at the approach of oviposition, apparently in a limited area near the genital sternite, probably from the oviduct, which is reported to be actively secretory at this time in various decapods (*cf.* Yonge, 1937, p. 507, and Ishikawa, 1885).

(4) *Oviposition:* To the excellent description of palaemonid oviposition by Höglund (1943), only a few details need be added. The eggs of *Palaemonetes* are emitted simultaneously from both oviducts, in a continuous stream. They emerge end to end, in single file, at the rate of about one per second per oviduct. They are of elongate, drop-shaped form when first extruded. The endopods of the first pair of pleopodites propel them to the anterior part of the incubatory chamber, but the rear is filled by gravity and pressure from the top of the growing pile, and the eggs in the chamber are not stirred about.

(5) *Fertilization: Fertilization* in *Palaemonetes* is external. The immotile spermatozoan of this and other Caridea does not exhibit the well-defined system of internal vesicles found in Reptantia (compare Nath, 1937, with Worley, 1939), and does not respond to hypotonic media by eversion. No reaction of the sperm-cell of *Palaemonetes* to contact with the eggs under a variety of circumstances has been detected, nor have any spermatozoa been found with the spike penetrant through the egg-membrane. It would be possible for a naked egg of *Palaemonetes* to capture and engulf a passive spermatozoan, at the moment of extrusion of egg from oviduct, before development of any membranes. Therefore, the hypotheses of entry of spermatozoa by an extraordinary torpedo-, plunger- or injector-like penetration of a poreless decapod egg-shell, proposed by previous investigators (Koltzoff, 1906; Binford, 1913; Needler, 1931; Bloch, 1935), seem unnecessary for Caridea. With regard to other groups, the only circumstantial description of actual entry of the spermato-

zoan, that for a pagurid by Bloch (*l. c.*), is weakened by an accompanying circumstantial account of what seem misapprehensions concerning the development of the egg-membranes, as well as by certain internal contradictions. It is therefore here suggested, as the solution of this long-debated question, that entry of the sperm-cell precedes development of the egg-membranes in all decapods. The function of the vesicular system of the reptant spermatozoa thus remains to be determined.

(6) *Attachment of the Eggs:* In *Palaemonetes*, the eggs are not adhesive when laid, and first become adherent to each other about half an hour after spawning. No free adhesive material exists in the brood-chamber, and no sign of attachment-substance other than the interfused first membrane of the eggs can be discovered. Extracted ovarian eggs become adherent to each other in the same manner as those laid and carried normally, although their development of fusibility and ductility is somewhat less in degree. Not only is egg normally attached to egg by this sole means, but attachment to the mother also is effected only by interfusion of the adjacent egg-membranes around the special unplumed incubatory setae, which are the only objects projecting into the brood chamber around which the eggs can meet to fuse.

The egg-stalks are drawn out by stretching movements of the pleopods of gradually increasing extent, beginning about half an hour after spawning. Attachment is completed in an hour, after which the pleopods are freely moved, not only for locomotion but in the rhythmic incubatory beat (which usually ceases only in highly aërated media or when no intact eggs remain attached to the pleopods).

Unmated females sometimes drop part or all of their eggs before attachment, by extension of their pleopods from the position of immobile flexion by which the brood-chamber normally is floored from spawning until attachment. Spawning otherwise proceeds as usual in unmated females, but after attachment the eggs are picked off by the chelae of the mother, none remaining after a few days unless the pereiopods have been amputated (in contrast to grooming in incubating mated females, which spares intact eggs whether fertile or not).

In fresh-water crayfish, the incubatory chamber becomes filled before spawning with a mucoid secretion which has been thought to serve for egg-attachment (Andrews, 1906). This phenomenon has been observed only in this group. In *Cambarus bartoni* this

mucoid material proves to differ in properties from the substance which forms the outer membrane of the eggs and is continuous and identical with that attaching them to the incubatory setae. Also, the mucoid material becomes precipitated upon other surfaces than those of attachment; and isolation of new-laid eggs with or without a portion of it does not result in their attachment to each other or to other objects.

Examination of the attached eggs of a variety of decapods of all groups (including *Lucifer,* the only incubatory peneid, in which the eggs are attached to a patch of microscopic spinules on the coxa of the third leg just distal to the opening of the oviduct) reveals no fundamental difference from the mode described for *Palaemonetes vulgaris* (Mode A), except that in many species egg does not become attached to egg but only to incubatory setae (Mode B). Closely related forms often differ in this respect (*e.g., Palaemonetes vulgaris* and *P. exilipes, Homarus* and *Cambarus, Pentacheles* and *Panulirus*). The Lereboullet-Yonge hypothesis (Yonge, 1937), of attachment by cement poured out into the brood-chamber by pleopodal glands and coating the entire egg to form its outermost membrane can hardly account for the lack of adherence of egg to egg in the tightly packed mass of new-laid ova found in such forms as *Cambarus, Panulirus,* the Brachyura, etc.; and therefore, in addition to its other deficiencies, this hypothesis would require highly distinct mechanisms of attachment in nearly related forms. It must, however, be noted that the discharge of the pleopodal glands during egg-attachment, described in *Homarus* by Yonge (*l.c.*) and by Lloyd and Yonge (1940), also occurs in *Palaemonetes;* although in the latter form it has been made certain by direct observation that the product of the glands is not a visible adhesive substance.

The Williamson-Broekhuysen hypothesis (Broekhuysen, 1936), of cement released from the vitelline space by bruising of the egg-shell can not account for the identity of the attachment-substance with the outer membrane of the eggs without losing its ability to explain Mode B; and does not account for the failure of eggs to be effectively bruised by such objects as, *e.g.,* the naked and the feather-like setae, which are interspersed with the brush-like incubatory setae to which the eggs are exclusively attached (by embedding of the tips of the setulae of the brushes in the first membrane), in *Cambarus shufeldti.*

The suggestion of Herrick (1911, p. 308), that if cement is

applied to the egg in the oviduct (as thought by Cano and Bumpus) "some other chemical products would seem to be needed to render this effective," is a hint of the true event.

A single hypothesis consonant with all known facts of decapod egg-attachment is as follows: The eggs of different decapods vary in the extent to which an enzyme-like secretion, released among them by the mother from the pleopodal glands during attachment, is required for the full expression of processes which are inherent in the first vitelline membrane and become functionally apparent as temporary self-fusibility. In forms where the eggs do not become attached to each other, the development of self-fusibility requires a degree of exposure to the intensifier-substance such as is obtainable only in the near neighborhood of the sources of this secretion on the incubatory setae.

(7) *Hatching:* In *Palaemonetes vulgaris,* the protozoeal molt skin is somehow freed from the parts which it still clothes, while the embryo is still tightly crammed into the intact egg-capsule shortly before hatching. Hatching begins by a rupture of the outer two membranes in a small area approximately over the embryonic labrum, diagonally opposite the point where the third membrane is cemented to the second. This point of rupture is probably determined early, by localized secretory activity applied to the second membrane while the third is developing. The hatching embryo, still enclosed by the intact, non-turgid, third membrane, is squeezed out through the constricting hole in the outer capsule in the course of half an hour, and hangs in the third membrane from the crumpled outer capsule for some time before it tears this final vestment off by a vigorous extension of the pleon. The pressure responsible for rupture of and emergence from the outer capsule appears to be developed wholly within the embryo itself, without obvious muscular action, possibly by imbition of water. Hatching can take place even after considerable sugar has been dissolved in the saline medium, and is not obviously hastened by distilled water.

In the fresh-water species, *Palaemonetes exilipes,* the process of hatching differs markedly in that the outer capsule is ruptured and rapidly squeezed off by the development of an interspace between third membrane and embryo. The third membrane continues to swell away from the embryo while hanging from the crumpled outer capsule, and finally bursts. The mechanism in *P. exilipes* therefore appears to be discharge of an osmotic agent

by the embryo at the appropriate time. The possibility is thus exposed, that the presumed hatching-uptake of water by the embryo itself in *P. vulgaris* might be by chemical means rather than by a mechanical one such as swallowing.

Although, as Panouse (1946, p. 122) has remarked, the precision of the relationship between termination of hatching and occurrence of the maternal post-incubatory molt does suggest the possibility of sensory mediation, it should be noted that the affirmative conclusions of Hess (1941) seem to be in conflict with the results of Nouvel and Nouvel (1937).

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A MUTANT IN DROSOPHILA MELANOGASTER AFFECTING FERTILITY AND EYE COLOR

As the result of x-ray treatment a mutant, called "deep orange" because of its effect on eye color, has been obtained in *Drosophila melanogaster*. Located at 0.0 ± on the X chromosome, the recessive gene causes a definite reduction in viability and has an effect on fertility similar to that reported by Lynch for fused.

Females homozygous for deep orange deposit eggs of normal appearance which fail to hatch if fertilized by spermatozoa from deep orange males. Approximately 100 eggs from this cross were dechorionated and examined after development had ceased in order to determine the extent of differentiation. Unlike the results of Poulson's work on small deficiencies at the notch locus, no characteristic stage of development was reached. Development stopped at any point from early cleavage up to the larval stage, and even two larvae were found. In nearly all cases the differentiation appeared to be abnormal.

If, however, the eggs of homozygous females were fertilized by the X spermatozoa of wild type males, a small number of heterozygous females were produced. The complete absence of males indicated that the Y spermatozoa were unable to initiate development. Nevertheless, all eggs from heterozygous females developed when fertilized by the deep orange males, which were apparently normal in fertility, even though half the eggs contained only the deep orange gene after meiosis. Thus development was not solely dependent on the genotype of the zygote.

Although the effect has been classed as maternal (Dobzhansky), development seems to hinge on the presence at some stage of the normal allele of deep orange, as Lynch pointed out for fused. In the eggs of heterozygous females the normal allele may take effect either prior to meiosis, from the polar body nuclei or from cells other than the oocyte—although Clancy and Beadle have apparently ruled out the latter by transplantation experiments with fused ovaries. On the other hand, the introduction by fertilization of the normal X allele into the eggs of homozygous deep orange females is able to initiate normal development. Although this behavior seems to indicate a deficiency of some sort, examination of the salivary chromosomes revealed that it was not chromosomal.

The problem thus is presented of a mutation which is actually a genic deficiency in that it can not do what the normal gene can in causing development. However, the effect of the normal gene, probably induced prior to meiosis, persists in the absence of the gene itself through the entire development of an egg into an adult, but is apparently unable to survive subsequent gametogenesis. The exact nature of this type of so-called genic deficiency remains to be determined.

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